Ecosystem services provided by *Modiolus modiolus* biogenic reefs

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Abstract

Ecological field studies were carried out *in situ* on *Modiolus modiolus* biogenic reefs throughout the UK to quantify the functional importance of these habitats and the associated ecosystem services that they provide to society. Using a combination of techniques, including Underwater Visual Censuses (UVCs), video transects and pot fishing, the key species associated with *M. modious* reefs were found to be *Buccinum undatum* and *Aequipecten opercularis*. *B. undatum* catches were three times higher on the *M. modiolus* reefs compared to adjacent habitats and the UVCs showed that *A. opercularis* were five times more abundant on *M. modiolus* reef sites. By providing a habitat for these commercially important shellfish, *M. modiolus* reefs act as an Essential Fish Habitat and support sustainable livelihoods.

M. modiolus are ecosystem engineers and can occur as dense aggregations, which form raised, three dimensional reef structures on the seabed. A new method was developed to measure *M. modiolus* biodeposition rates *in situ* and this provides the first evidence of the scale at which *M. modiolus* are able to enhance sedimentation and contribute to the downward flux of material to the seabed. *M. modiolus* biogenic reefs are recognised as biodiversity hotspots and protected in Marine Protected Areas. However, under controlled conditions when subject to seawater temperatures above those experienced in the wild, byssus thread production is compromised whilst biodeposition rates are modified also.

M. modiolus reefs at the southern limit of their known distribution will continue to exist in the short term but with predicted increased seawater temperature, *M. modiolus* may not be able to function to their full ability. These habitats are vulnerable to physical impact from mobile fishing gear and the results presented here suggest that reef recovery through byssus attachment and clump formation would be limited, especially in southern populations. Management of protected reefs should take this into account and ensure that ecosystem resilience is maximised through well enforced management measures.

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Chapter 1. General Introduction

The horse mussel, *Modiolus modiolus* is a large filter feeder and individuals occur on both sides of the Atlantic, from the Arctic to the Bay of Biscay (Hayward and Ryland 2006, Gormley 2013, Rees 2009). *M. modiolus* can form dense aggregations, known as 'biogenic reefs', and as far as we know, the southernmost reefs on the eastern Atlantic are located off North Wales in the Irish Sea (Figure 1). Here, the reefs are of considerable size; reef height is approximately 1 meter above the under-lying gravel substratum and the area covered is approximately 600 hectares in total (Lindenbaum et al. 2008). A similar formation has also been described in the north east of Scotland (Hirst et al. 2012a) and smaller beds occur in west coast sea lochs and in Orkney and Shetland (Mair et al. 2000, Sanderson et al. 2014). The three dimensional reef structures are composed of a matrix of dead shell, biodeposits and byssus threads with live mussels and associated fauna on the reef surface.

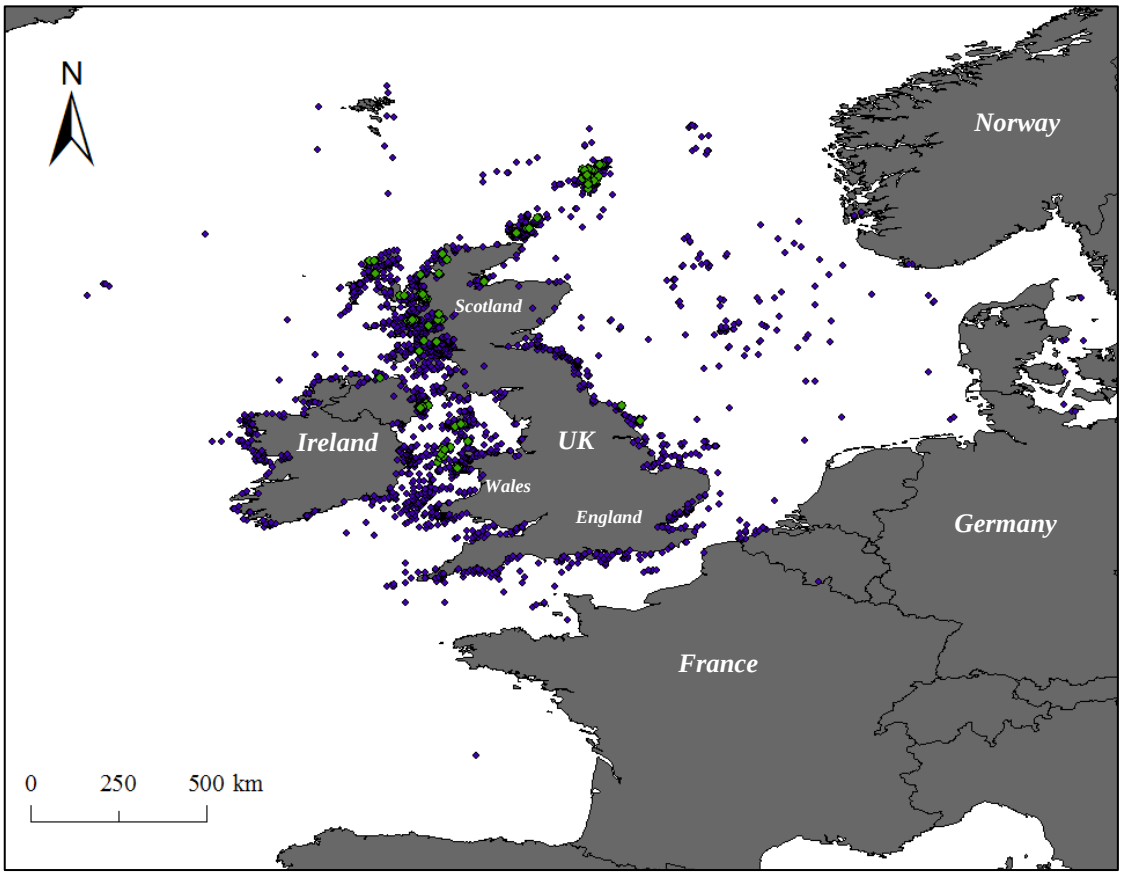

Figure 1. Distribution of *M. modiolus* in Europe. Blue circles = individual *M. modiolus* records (Gormley 2013), green circles = *M. modiolus* beds (Rees 2009).

Biogenic reefs, such as those formed by *M. modiolus* are biodiversity hotspots (Rees et al. 2008, Sanderson et al. 2008), and recognized for their conservation importance. They protected as "reefs" in Special Areas of Conservation (SACs) under Annex I of the EC Habitats Directive. *M. modiolus* reefs are also a Priority Marine Feature (PMF) in Scotland, protected in 4 Nature Conservation Marine Protected Areas (NC MPAs). *M. modiolus* habitats in the 'reef' formation can also be described as 'beds' and according to the OSPAR Commission (2009), patches that are greater than $10m^2$ with over 30% cover of live mussels can be classed as a bed.

The largest known *M. modiolus* reef in the UK is the Noss Head reef in north east Scotland which covers 450 ha (Hirst et al. 2012a). Biodiversity on *M. modiolus* reefs is high, with 278 species recorded on a reef in Scapa Flow in Orkney (Hirst et al. 2012b) and up to 619 *M. modiolus* per m^2 on the reefs in North Wales (Rees et al. 2008). However, very little is known about the functional importance of biogenic reefs and the ecosystem services that they provide to society. One approach that is becoming increasingly popular is to characterise an ecosystem in terms of 'goods and services'. The term Ecosystem Goods and Services (EGS) can be defined as "the direct and indirect benefits people obtain from ecosystems" (Beaumont et al. 2007), and may be used to highlight how useful the sea is for us. EGS can be split into five categories; production services, regulating services, cultural services, option use value and over-arching support services (Millennium Ecosystem Assessment 2005).

Ecosystem Goods and Services

Biodiversity is fundamental in the provision of ecosystem goods and services. The rate and efficiency of processes that marine organisms carry out are determined by the interactions between organisms and between the organisms and their environment. Thus, a relationship between biodiversity and ecosystem function has been observed (Heip et al. 2009, Naeem et al. 1994); with highly diverse ecosystems performing functions at a higher level and ultimately providing important ecosystem services to society. Figure 2 shows a framework used by de Groot et al. (2002) to value systems based on biodiversity, ecosystem function and ecosystem services, and how this can feed into policy.

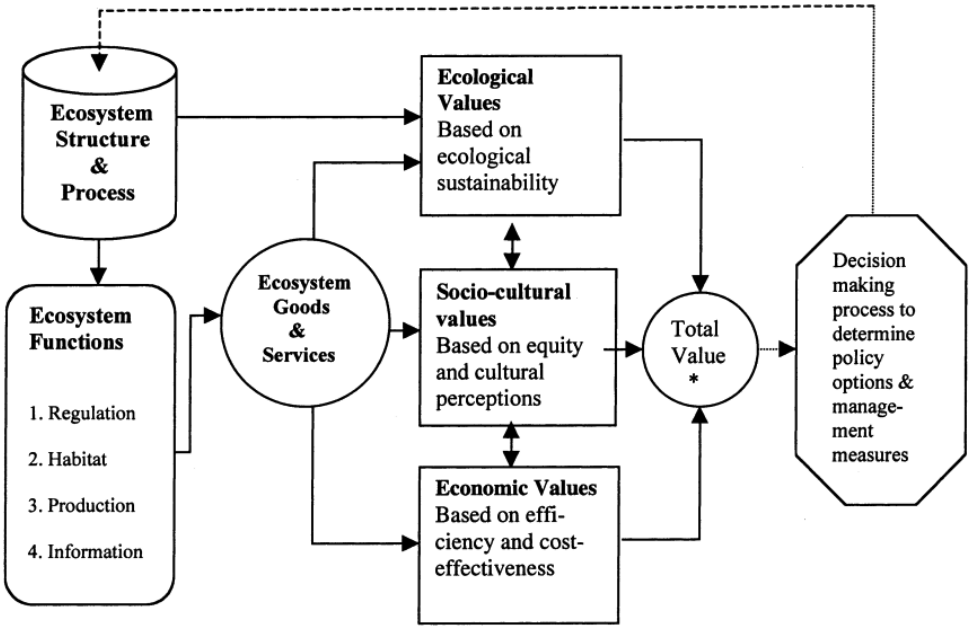

Figure 2. Framework for the assessment and valuation of ecosystem functions, goods and services (de Groot et al. 2002).

Highlighting and quantifying the services provided by different marine ecosystems can help translate the complexity of these environments into a list of ecosystem functions that can be more easily understood by policy makers. Ultimately this shows the relative value of different habitats and species to society, which can support decision making and marine spatial planning.

Protection and restoration of habitats can enhance biodiversity and ecosystem functions, and therefore enhance the crucial ecosystem services provided by these ecosystems. Micheli & Halpern (2005) show that recovery of species diversity in marine reserves increases functional diversity, which is a key driver of ecosystem processes. Understanding the relationship between biodiversity and ecosystem function is vital in order to achieve sustainable exploitation of living marine resources (Heip et al. 2009).

The key studies on biogenic reef ecosystem services to date largely focus around oyster reefs. There has been a great deal of research on the ecosystem services provided by oyster reefs in the USA, in support of the large scale restoration of oyster reefs for example in Chesapeake Bay, e.g. Kellogg et al. (2011) and Grabowski and Peterson (2007). Little research on biogenic reef ecosystem services has been carried out on the

eastern side of the Atlantic and the majority of studies that have been carried out, focus on the services provided by maerl beds (Kamenos et al. 2004b). A review of the literature on biogenic reef ecosystem services in the North East Atlantic highlights some services for which biogenic reefs are particularly relevant and this has been summarised in table 1.

Table 1. Examples of ecosystem goods and services provided by biogenic structures in the North East Atlantic (modified from the Millennium Ecosystem Assessment, 2005). Services in bold indicate those studied in the present thesis.

Category	Ecosystem service	Benefits	Reference
Production	Shell fish food Raw materials (shells used in road construction, jewellery etc., maerl extracted for water purification, cosmetics etc.)	Food Transport	Grall and Hall-Spencer (2003).
Regulating	Bioremediation of waste and water filtration Gas and Climate regulation **Sediment stabilisation** and coastal protection	Clean safe water, Clean air, Safe place to live	Gray et al. (2000); Grall and Hall-Spencer (2003); Holt et al. (1998)
Cultural	Fishing Diving	Recreation and leisure	
Over-arching support	**Essential Fish Habitat** **Nutrient sequestration** Bentho-pelagic coupling Reduction of turbidity	Support other services	Kamenos et al. (2004c); Yeager and Layman (2011); Kellogg et al. (2011)

The following section focuses on four ecosystem services and describes the functional role that *Modiolus modiolus* reefs would be expected to have in providing these services. The services are chosen based on their relevance to *M. modiolus* habitats and the results of previous studies on similar habitats such as oyster reefs (Kellogg et al. 2011) and maerl beds (Kamenos et al. 2004b). The ecosystem services chosen are: Essential Fish Habitat; nutrient cycling; sediment stabilisation and accumulation (through active and passive processes); and reef formation (through byssus thread attachment).

Essential Fish Habitat

Globally, fish stocks are under threat due to over-exploitation of marine resources (Jackson et al. 2001) and action is required to halt this trend and restore fish stocks (Worm et al. 2009). A shift to 'Ecosystem-Based Management' (EBM) for fisheries involves a move from traditional single species based management to a deeper understanding of the complex interactions between habitats and commercially important species that are associated with them. This approach has been carried through into the EU Common Fisheries Policy in order to fall in line with the Marine Strategy Framework Directive (MSFD) (Commission COM 2009).

The EBM approach extends the focus of managing resources beyond the target species and includes impacts to non-target species and benthic habitats. Further to this, EBM aims to support ecological processes that are required to sustain harvestable resources (Hughes et al. 2005). Ecosystems are central to the MSFD, which seeks to manage the marine system as a whole, for example through descriptor 6: "Sea-floor integrity is at a level that ensures that the structure and functions of the ecosystems are safeguarded and benthic ecosystems, in particular, are not adversely affected" (JNCC 2010). However, in reality marine activities are often managed by sector-specific policies and are rarely considered within a single system (Ounanian et al. 2012).

In America, the ecosystem approach was reinforced in 1996 when the United States made amendments to the Sustainable Fisheries Act (SFA) and required all fisheries management councils to identify the 'Essential Fish Habitat' (EFH) for commercially important fish species (Fluharty 2000). US congress defined EFH as "those waters and substrate necessary to fish spawning, feeding or growth to maturity." This approach aims to identify, conserve and restore fish habitat in order to sustain healthy fish stocks.

Demersal fish in particular, rely on certain habitat features throughout their lives, to grow, reproduce and survive (Gibson 1994). The EFH concept is not confined to describing finfish habitat associations; it has also been used for invertebrates, e.g. conch (Glazer and Kidney 2004) and octopus (Garofalo et al. 2011) and even marine mammals such as the bottlenose dolphin (Ingram and Rogan 2002).

Identifying a habitat as an EFH is not a simple task, especially for highly mobile species that use a range of habitats throughout their life cycle. With limited resources, conserving or restoring every habitat used by a fish is unrealistic, therefore identifying habitats that are used during sensitive life stages are often prioritised (Levin and Stunz 2005). Restored shellfish reefs have been found to be EFH for commercially important fish (Scyphers et al. 2011). However, it is important to distinguish between the artificial reef (created by deploying cultch in restoration) acting as a fish aggregation device, attracting mobile species from surrounding areas due to behavioural preferences, and a habitat that actually enhances the overall production of fish (Bohnsack 1989). As a consequence, artificial reefs can have a deleterious effect of fish abundance by concentrating the biomass in one area and making them more accessible for fisheries and therefore vulnerable to overexploitation (Grossman et al. 1997).

In order to distinguish between the fish aggregation function of a reef structure and true EFH it is important to consider the functional role of the habitat for mobile species found on biogenic reefs. For example, specific habitats are required for reproduction in gastropods (Glazer and Kidney 2004) and juvenile queen scallops preferentially attach to biogenic structures compared to gravel or sand and this preference has been shown to be a predetermined behavioural trait rather than a predator avoidance tactic (Kamenos et al. 2004a). Oyster reefs have been found to provide an important role in the energetic requirements of certain fish species (Yeager and Layman 2011) and Pearce et al. (2011) found that the reef building Ross worm (*Sabellaria spinulosa*) contributed a significant proportion of the diet of flatfish, including Dover sole, dab and plaice.

Given the fact that biogenic habitats in the UK have been found to have an EFH role (e.g. maerl and *Sabellaria* reefs as mentioned above), it is therefore expected that *M. modiolus* reefs may provide a similar function. However, *M. modiolus* habitats are relatively inaccessible and their ecological function is understudied, therefore information on the EFH role of *M. modiolus* reefs remains unknown.

Nutrient Cycling

In oyster reef ecosystem function research, a great deal of attention has been focused on nutrient cycling and water filtration (Kemp et al. 2005), due to severe hypoxia events that have occurred in Chesapeake Bay, which has caused loss of seagrass and benthic invertebrates. Oysters not only act as a top-down control on phytoplankton growth but also increase denitrification, which counteracts eutrophication. Kellogg et al. (2011) studied biogeochemical cycling on oyster reefs and found that the annual denitrification rate for restored reefs was almost 12 times higher than for unrestored reefs, and 384 times more nitrogen was sequested on restored reefs than unrestored reefs per unit area. Samples from the restored reef were found to contain 1062 times more carbon than the non-restored reef.

Maerl is an effective water filter (Gray et al. 2000), and meal beds are able to remove nutrients such as phosphorus and nitrogen from the water column, and are therefore important for nutrient cycling and bioremediation of waste. Maerl has been extracted since 79 AD and used as soil fertilizer, and it is still used for water purification, mineralization and in the manufacture of cosmetics. Maerl extraction reached 600 000 tonnes yr^{-1} in Brittany in the 1970s (Grall and Hall-Spencer 2003).

As *M. modiolus* are large filter feeders, it is expected that the capacity for *M. modiolus* reefs to enhance biogeochemical cycling and the sequestration of nutrients is similar to that of oyster reefs (Kellogg et al. 2011). Over time, dense aggregations of *M. modiolus* create raised beds approximately 1 meter high (Lindenbaum et al. 2008) and it has been suggested that the build-up of *M. modiolus* shell material makes an important contribution to carbon sequestration (Burrows et al. 2014).

Sediment Stabilisation and Accumulation

Organic material on a reef largely originates from phytoplankton that sink from the upper photic layers of the water column to the seabed, as do dead zooplankton and faecal pellets. Benthic sediment can become resuspended by physical mixing and this can enhance production in the water column (Doering 1989). Also, mobile fauna may deposit organic material on a reef that they use for shelter at night after feeding in surrounding areas (Bray et al. 1981), which further increases the flow of organic material onto the reef.

The presence of biological organisms on the seabed often structures a habitat in a way that increases sediment stabilisation by the accumulation of material around the organism. For example, saltmarsh plants provide structure to fine sediments and enhance sediment accretion (Adam 1990), mangrove roots stabilise sediments and are key to the sedimentation process (Carlton 1974) and oysters provide stabilisation for adjacent habitats (Grabowski and Peterson 2007). It is therefore expected that as habitat forming species, *M. modiolus* provide a similar function in sediment stabilisation and accumulation.

Biodeposition and Filter Feeding

Filter feeders use cilia to create a flow of water into the inhalant siphon where particles are captured and transported towards the mouthparts (Ward and Shumway 2004). In *M. edulis,* unwanted material is rejected by the palps and at high food concentrations, the palp food groove becomes narrow, forcing material out onto the rejection tract (Foster-Smith 1975). The product of this material is called "pseudofaeces" and it usually forms a continuous string.

Biodeposition is a term used to describe faeces and pseudofaeces together as a total unit, produced by a filter feeder. Pseudofaeces are particles that are rejected before ingestion, whereas faeces are formed by the ingestion of particles through the feeding structures of a filter feeder, which are packaged into faecal products. As a result of this selection process, faeces and pseudofaeces differ in their size, shape and organic properties (Graf and Rosenberg 1997, Navarro and Thompson 1997).

In order to measure the natural water filtration function deployed by filter feeders, many authors measure clearance rates (Pascoe et al. 2009). Clearance rate calculations are based on the decrease in concentration of particles in a known volume of water that contains a filter feeder over time, and this calculation can be adjusted for open systems with a constant flow rate. Clearance rates are usually standardised for the size of the animal because smaller animals have higher weight specific filtration rates (Foster-Smith 1975, Tsuchiya 1980). However, there are many assumptions made when calculating clearance rates (Coughlan 1969) and when attempting to estimate feeding rate, error may arise if these assumptions are not met. According to Coughlan (1969), the method assumes that 1) there is no gravitational settling of particles in suspension;

2) particle retention is 100% efficient; 3) the animal's pumping rate is constant; and 4) the test suspension is homogeneous at all times. Clearance Rate calculations should be used as a relative indication of feeding rate rather than an absolute measure.

Given the uncertainties that arise from the clearance rate method (Coughlan 1969), many subsequent authors opt for methods that take into account the amount of organic material produced as faeces to calculate a more realistic measure of ingestion rate. This is known as the 'biodeposition method' (Iglesias et al. 1998), however, this method does not take into account pseudofaeces production and is therefore appropriate for energetics studies but not for measuring the flux of material to the seabed.

Numerous studies have found that particles are selected by filter feeders based on their diameter and suggest that this is the result of a sieving mechanism, however, capture efficiency is also species specific. For example, Palmer and Williams (1980) found that the scallop (*A. irradians*) is less efficient at capturing particles <7µm than the oyster *C. virginica.* Hawkins et al. (1998) found that epifaunal species such as *M. edulis* demonstrate a higher capacity to selectively ingest organic material compared to *C. edule,* an infaunal species. Alternatively, Kiorboe and Monhlenberg (1981) suggest that the size of the labial palps determines selection efficiency in bivalves.

There is some debate as to whether the filtering mechanism employed by bivalves is purely an "on or off" automated process (Jørgensen 1996, Saraiva et al. 2011) or if there are more advanced physiological processes involved. For example, Bayne (1998) argues that filter feeding in bivalves is a complex interaction involving behavioural, physiological and morphological traits to achieve optimal absorption efficiency when exposed to a high variation of food quality and quantity. Lopes-Lima et al. (2014) go further to suggest that *Anodonta cygnea* (a freshwater mussel) is able to select food in response to its nutritional characteristics and that this selection process is associated with the mussel's physiological life cycle. This was based on an investigation into the stomach contents of *A. cygnea* and although *A. cygnea* generally ingested algae in a similar pattern to its abundance in the water column, blue green algae were preferentially selected during periods of gamete development. De Mott (1993) describes this 'decision-based selection' in certain filter feeders whereby captured particles appear to be tasted at the mouth before being ingested or rejected. Furthermore, De Mott (1993) also highlights the importance of hunger or fullness when comparing laboratory

and field experiments as food can become limited in natural conditions whereas laboratory experiments often test high concentrations of food, which may influence how hungry the mussel is during long-term experiments.

The active process of filter feeding and the resulting biodeposition is expected to be a significant contribution to the overall accumulation of sediment on a mussel bed. This is partly due to the sheer volume of water that bivalves are able to filter but also the change in physical structure of the sediment-water interface created by the presence of the benthic organisms (Graf and Rosenberg 1997). Because biodeposits are rich in carbon and nitrogen, this downward flux of material from the water column to the seabed can significantly alter the physical and chemical properties of the seabed (Miller et al. 2002).

Navarro and Thompson (1996) found that *M. modiolus* are able to filter 1-4 litres per hour and the highest ingestion rates were in April-May during the spring bloom when water temperatures are low (0°C), but phytoplankton abundance is high. Further experiments using flow through chambers supplied with natural seston show a maximum biodeposition rate of 40.9mg dry weight per day for a 5g mussel (Navarro and Thompson 1997). During the spring diatom bloom, faeces production was five times greater than pseudofaeces however, after the spring bloom faeces production decreased dramatically until the mussels stopped producing pseudofaeces altogether.

Reef Formation

For a *M. modiolus* reef to form, the environmental conditions must be appropriate (e.g. seawater temperature, adequate food supply and substrate type etc.) and there must be a sufficient supply of *M. modiolus* larvae to sustain the population (Gormley et al. 2013). However, it is expected that byssus threads also play an important role in reef formation because byssus threads are used to hold mussels together to form *M. modiolus* 'clumps' and juvenile *M. modiolus* are often found amongst adult byssus threads (Fariñas-Franco et al. 2013).

In comparison to the feeding mechanism in bivalves, byssus thread production has received very little attention in the literature despite the ecological importance of these structures. Byssus threads are secreted by the foot and act to guy the mussel in place by attaching to the substrate or other animals, with an adhesive disc at the end of each

thread (Gosling 2003). These structures have incredible tensile strength and shock absorbing characteristics which make them very effective at anchoring the mussel to the seabed (Smeathers and Vincent 1979). The strength of *Mytilus edulis* byssus threads varies seasonally, being 60% stronger in the spring and it is suggested that thread quality is reduced during periods of low food availability and that high temperatures may impair the molding process that occurs during thread production (Moeser and Carrington 2006).

It is commonly thought that byssus threads are made from a substance that is similar to collagen due to their resemblance to hair. Indeed, Smeathers and Vincent (1979) describe the byssus as a "continuous fibrous structure, with new threads added at the base of the stem to replace older broken threads at the distal end of the stem". The exact function of byssus threads varies from species to species depending on the typical habitat in which the mussel occurs. For intertidal organisms with a high probability of dislodgement due to wave action, byssus threads are produced in response to agitation in order to maintain a position on the shore (Young 1985). However, Bell and Gosline (1997) found that *Mytilus trossulus* typically form dense clumps in the wild, and these aggregations provide some protection for individual mussels from hydrodynamic forces. It is therefore postulated that this aggregation behaviour is the reason that *M. trossulus* have thinner threads than *Mytilus californianus,* which is usually found on highly exposed shores.

For reef forming species, byssus threads are often used to attach to sediment grains or other mussels and this process is a fundamental step in reef formation. Meadows and Shand (1989) found that *M. modiolus* produce more byssus threads than *M. edulis* when held in sediment and threads created by *M. modiolus* are also longer, especially in fine sediments. This highlights the significance of subtidal mussels in bioengineering sediments, and reducing erosion. It is therefore expected that the production of byssal material is an important process for an ecosystem engineer such as *M. modiolus.*

Anthropogenic Impacts on Marine Ecosystems

The marine environment is subject to a number of human activities, many of which have altered the structure and function of marine ecosystems. Since the 1980s the scale of our impact on marine ecosystems through fishing activities has become apparent across a range of habitats (Jackson et al. 2001). MPAs are seen as an important

management tool to conserve species and habitats (Tundi Agardy 1994) and over time, well managed MPAs can provide ecological and societal benefits (Fox et al. 2012). Marine Reserves for example, can enhance the biomass of fish species within closed areas and create a spill-over effect (Francini-Filho and Moura 2008). Protected areas can also expand recreational activities and provide educational opportunities (Angulo-Valdés and Hatcher 2010). However, the benefits provided by ecosystem services are often acknowledged at different spatial scales, e.g. carbon sequestration provides a benefit on a global scale, whereas enhanced fisheries production is valuable on a local scale (Fox et al. 2012).

There is increased interest in the relationship between biodiversity and ecosystem function given the wide scale loss of biodiversity in marine ecosystems (Worm et al. 2006). Further to this, an increasing human population results in an ever-growing demand for ecosystem goods and services. Therefore, ecologists have joined forces with economists and social scientists to study the change in the provision of services by ecosystems in response to human impacts. For example the impact of climate change (Bulling et al. 2010) and habitat loss (Dobson et al. 2006, Morris 2010) on ecosystem service provision. However, the societal problems associated with biodiversity loss depends on the trophic level of the key species responsible for the service in question. Although there is more interest in protecting top predators, it is usually the species at low and intermediate levels (e.g. bacteria and algae) that support the majority of the services (Dobson et al. 2006).

Research has shown that stressors such as climate change and mobile fishing gear can influence biogenic reef distribution (Gormley et al. 2013) and structure (Hall-Spencer and Moore 2000). However, few studies address the subsequent loss or modification of ecosystem services provided by these habitats.

Ecosystems are often subject to multiple stressors and the impact of these factors on the provision of ecosystem services are often measured independently, for example, invasive species (Katsanevakis et al. 2014), and benthic trawling (Muntadas et al. 2014). However, in reality, natural systems may be subject to many impacts simultaneously and the consequence of these can be additive, or the interaction between factors may be antagonistic and reduce the overall stress (O'Gorman et al. 2012).

Existing MPAs that are designated on an *ad hoc* approach and are unlikely to take into account the long term, large scale dynamics of marine ecosystems and Bengtsson et al. (2003) suggest that static reserves should be used in combination with dynamic reserves to cater for natural disturbance regimes. In addition to natural disturbance, extreme weather events are expected to increase with global warming and such events can have a significant impact on marine communities (Wernberg et al. 2013). The effects of extreme weather events are wide ranging but include increased ocean temperature, an increase in storm frequency and changes in salinity due to increased runoff (Rhein et al. 2013). However, predictions of how such conditions may change in the future are surrounded by a high level of uncertainty (Lowe and Gregory 2005).

Objectives and Thesis Structure

The two primary objectives of this thesis are given below:

Objective 1) Describe the key ecosystem services provided by biogenic reefs and quantify these services using *Modiolus modiolus* reefs as a model habitat. The ecosystem services focused on are provision of a habitat for fish and shellfish and sediment sequestration (through passive and active processes).

Surveys were carried out to investigate the key megafaunal species associated with *M. modiolus* reefs across the UK; the results of this study are presented in chapter 2. This study aims to test the hypothesis that there is a greater abundance of megafaunal species living on horse mussel reefs compared to control habitats. The habitat association concept was further developed using stable isotope analysis to look at the trophic structure of the reef community. Chapter 3 focuses on one key species associated with *M. modiolus* reefs identified in chapter two (*Buccinum undatum*), and investigates the spatial density and size distribution of this, commercially important species on the Pen Llŷn *M. modiolus* reef.

Following on from this, chapter 4 focuses on quantifying the functional importance of *M. modiolus* reefs for sediment sequestration, by taking measurements of sediment accumulation *in situ* on a *M. modiolus* reef on the west coast of Scotland. This involves the development of a method to separate the passive and active processes that contribute to the accumulation of sediment.

Objective 2) Investigate the impact of increased seawater temperature on *M. modiolus* biodeposition and byssus thread production and discuss the implications for the provision of associated ecosystem services (sediment sequestration and reef formation).

Chapter 5 describes the functional response of *M. modiolus* to a change in seawater temperature, with the response variables biodeposition and byssus thread production. Three experiments were carried out in an aquarium setting to test the hypothesis that horse mussel biodeposition rate and byssus thread production decrease at temperatures at the maximum of their biogeographical thermal range. The purpose of this final chapter is to investigate how the provision of ecosystem services by *M. modiolus* reefs might change in the future as environmental conditions change.

Chapter 6 discusses the findings of the experiments mentioned above and covers the cross-cutting themes demonstrated throughout this thesis. The results are described in a Marine Spatial Planning context for consideration in the creation and management of MPAs. Finally, the fate of *M. modiolus* reefs and the ecosystem services that they provide are considered in relation to changing climatic conditions.

Chapter 2. Key megafaunal species associated with *Modiolus modiolus* reefs

Abstract

Megafauna community abundance on *Modiolus modiolus* biogenic reefs was compared with off-reef sites that were either sand or cobble habitats. *In situ* counts of megafauna were carried out across the British Isles, in Orkney, Shetland and the Pen Llŷn in North Wales. The key species associated with *M. modiolus* reefs were scallops (*Aequipecten opercularis*), whelks (*Buccinum undatum*) and urchins (*Echinus esculentus*). Starfish (*Asterias rubens*) and spider crabs (*Maja brachydactyla*) were also abundant on the Pen Llŷn reef. Stable isotope analysis showed that *B. undatum* were one trophic level higher than *M. modiolus* and therefore could be feeding on the mussels and associated fauna. *A. opercularis* are more likely to be using the complex reef habitat as an attachment site during early life stages with subsequent permanent colonization. The results of this study have shown that, as well as being biologically diverse habitats, *M. modiolus* reefs are also functionally important in their role as an essential habitat for commercially important shellfish. *M. modiolus* reefs are fragile communities that face multiple pressures; therefore, appropriate protection and spatial management of *M. modiolus* reefs is vital in order to maintain this functional role.

Introduction

Modiolus modiolus reefs are typically characterised by high species diversity (Hirst et al. 2012, Sanderson et al. 2008, Rees et al. 2008). The distribution of *M. modiolus* habitats and associated flora and fauna has been studied and described in detail (e.g. Hinz et al. 2008; Moore et al. 2013). However, the relative importance of *M. modiolus* reefs as a habitat for megafauna has not been quantified.

Field studies have shown that restored, healthy oyster reefs support a greater biomass and diversity of megafauna compared to damaged reefs or control sites (Rodney and Paynter 2006, Stunz et al. 2010, Kellogg et al. 2011). Grabowski & Peterson (2007) highlight several ecosystem services provided by oyster habitats, including: production of oysters for food; provision of habitat for epibenthic invertebrates; carbon sequestration; fish production; and shoreline protection.

Experts advise that oyster reefs should be recognised as “Essential Fish Habitats” (EFH) (Coen and Luckenbach 2000) due to a close association between the reef and species of fish (e.g. gobies and blennies) and shellfish (e.g. grass shrimp). EFH is defined under the Magnuson-Stevens Act (NOAA 1966) and aims to identify habitats that are important for growth, reproduction and survival of fish in order to restore fish stocks. Able (1999) suggests four levels of assessment to determine whether a habitat is essential for a particular species: Level 1) presence/absence, level 2) relative abundance, level 3) relative growth, survival or reproduction rates, level 4) relative productivity. Using level 2 of this assessment, Peterson et al. (2003) predict that restored oyster reef can enhance fish and large crustacean production by 2.6kg yr^{-1} for every $10m^{-2}$.

As with *M. modiolus* reefs, maerl form subtidal, biodiverse biogenic structures in the UK. Kamenos et al. (2004b) found that maerl habitats are an important nursery ground for juvenile queen scallops (*Aequipecten opercularis*) and under laboratory conditions, *A. opercularis* find refuge within maerl crevices and are more likely to survive predation. Similarly, Jansson et al. (1985) found that blue mussel (*Mytilus edulis*) beds support a greater biomass of associated demersal fish fauna compared to control sites. Relative fish abundance measurements provide an initial insight into which areas are important for fish and shellfish and an investigation into the functional role of the habitat (e.g. nursery or feeding grounds), can provide further evidence for EFH.

A common issue with fisheries management is that information on fish populations is often collected using fishing trawl surveys in association with the fishing industry (Agardy 2000). Measuring fish abundance in marine systems is almost impossible without some sort of bias. Fishing gear is often highly selective (Dahm et al. 2002), the use of bait attracts some species more than others and the sampling area is usually unknown due to the unpredictable nature of a bait plume (Taylor et al. 2013). Therefore, baited fish counts are relative rather than absolute. Nevertheless, Essential Fish Habitat Suitability (EFHS) models can be created, using information on relative fish abundance in different areas, to prioritise areas of the seabed for protection (Trimoreau et al. 2013).

In order to measure the abundance of fish at different habitats, Underwater Visual Censuses (UVCs) can be used as these are non-destructive and independent of fishing gear bias. However, a problem with using UVC techniques is the ‘diver effect’ (the reaction of fish to a diver), with some fish being attracted to the diver and some repelled

(Dickens et al. 2011). Further bias can arise due to the size, mobility and crypsis of the fish species (Bozec et al. 2011). Most studies suggest that UVCs should be used in combination with other techniques to more accurately produce a fish census (Bennett et al. 2009).

UVCs have the advantage of divers being able to search in and around seabed structures compared to a stationary camera or trap. However cameras can be used to compliment diver visual counts along transects (Pelletier et al. 2011). Towed video cameras or Remotely Operated Vehicles (ROVs) are able to dive deeper for longer, and cover larger areas of the seabed than SCUBA divers. Morrison and Carbines (2006) highlight further advantages of using a towed video camera to measure fish communities, these include: a known area of the seabed can be sampled; habitat features can be measured; and lasers can be used to measure objects (e.g. fish size; Biber et al. 2014). Although some fish species may avoid the camera as it passes, the towed video technique provides an effective way to measure fish abundance and habitat associations with minimal bias (Spencer et al. 2005).

The community structure of *M. modiolus* reefs has been studied comprehensively (Mair et al. 2000, Moore et al. 2013, Rees 2009) however, the trophic structure of *M. modiolus* reef communities is unknown. Stomach content analysis is commonly used in food web analysis to describe the diet of fish and invertebrates. However, when studying juvenile fish and smaller invertebrates the food items can be hard to identify and at certain times of year, many of the stomachs are empty (Kamenos et al. 2004c), therefore alternative methods are often required.

Stable isotope analysis can be used in combination with stomach content analysis and is seen as a rigorous method becoming a popular method for studying food webs (Schaal et al. 2012). Carbon isotope ratios track the flow of carbon in an ecosystem. Most carbon exists as ^{12}C although ^{13}C also exists and the ratio of the two isotopes ($\delta\,^{13}C$) is altered by biological processes. The $\delta\,^{13}C$ from the tissue of an animal indicates the source(s) of carbon at the base of the food web and therefore provides an indication of the animal's diet. On the other hand, ^{15}N becomes enriched during trophic transfers, therefore analysis of $\delta\,^{15}N$ and $\delta\,^{13}C$ together can be used to determine the food chain length in a system, the feeding mechanisms used and the isotopic variance of an

organism. This can also be used to understand trophic cascades (Grabowski 2004) and bentho-pelagic coupling (McIntyre et al. 2006).

Yakovis et al. (2012) used stable isotopes to show that horse mussels and ascidians growing together have distinct diets and there is no overlap in the origin of their food. Maerl beds are also diverse biogenic structures and Grall et al. (2006) were able to distinguish between the trophic groups in a maerl community, based on the range of feeding mechanisms utilized, which were determined using stable isotope analysis. Yeager and Layman (2011) used stable isotope analysis to show that oyster reefs are essential habitats for the grey snapper (*Lutjanus griseus*) and the crested goby (*Lophogobius cyprinoides*). The fish were feeding on benthic invertebrates from the reef and analysis of relative $\delta^{13}C$ values showed that this food was originating from microphytobenthos and seston. It is expected that resuspended benthic diatoms, phytoplankton and Particulate Organic Matter (POM) will be the main sources of carbon in the food chain on a *M. modiolus* reef.

The aim of this study is to determine the importance of *M. modiolus* reefs as an Essential Fish Habitat. I*n situ* observations of megafauna were used to test the hypothesis that megafauna (defined here as animals greater than 2cm maximum length) are more abundant on *M. modiolus* reefs than on control habitats (sand and cobble). The trophic levels in a *M. modiolus* reef community will be determined using stable isotope analysis.

Methods

Megafauna abundance surveys were undertaken in three UK regions; Orkney, Shetland and Pen Llŷn (Figure 3 A). Underwater Visual Censuses (UVCs) were carried out at 23 sites in Shetland and Orkney, 15-25m below chart datum (Figure 3 B and C). A two meter pole was used to ensure a constant belt width was maintained along each 30m transect (Figure 4 A). The Pen Llŷn *M. modiolus* reef (Figure 3 D) was impractical to survey at multiple sites due to strong currents. Therefore a drop down video camera system was used to count megafauna on the reef and at control sites adjacent to the reef. Sites were selected based on the known extent of *M. modiolus* reefs in the UK and the three areas (Shetland, Orkney and the Pen Llŷn) were chosen to cover a range of environmental conditions for the known distribution of *M. modiolus* reefs (Figure 1).

Sites in Orkney were surveyed in May 2013 and sites in Shetland were surveyed in September 2012. The sites were selected at random from drop down video (DDV) footage or from previous dive data within either reef, sand or cobble habitats. Some DDV sites were inappropriate to survey using SCUBA divers due to depth and current constraints, therefore these sites were chosen at a nearby, more suitable area. Eight biogenic reef sites were sampled, each with a density of *M. modiolus* greater than 20 mussels per m^2. Off-reef sites included sandy habitats (8 sites), and cobble habitats (7 sites). All observers were trained in species identification during a pilot study in May 2012 in Orkney where 12 sites were visited. During the training survey, 9 species of megafauna were recorded including gobies (e.g. *Pomatoschistus pictus*), scallops (*Aequipecten opercularis*), whelks (*Buccinum undatum*) and urchins (*Echinus esculentus*) and sites covered *M. modiolus* reef, sand, maerl and rocky habitats (appendix A1 and A2).

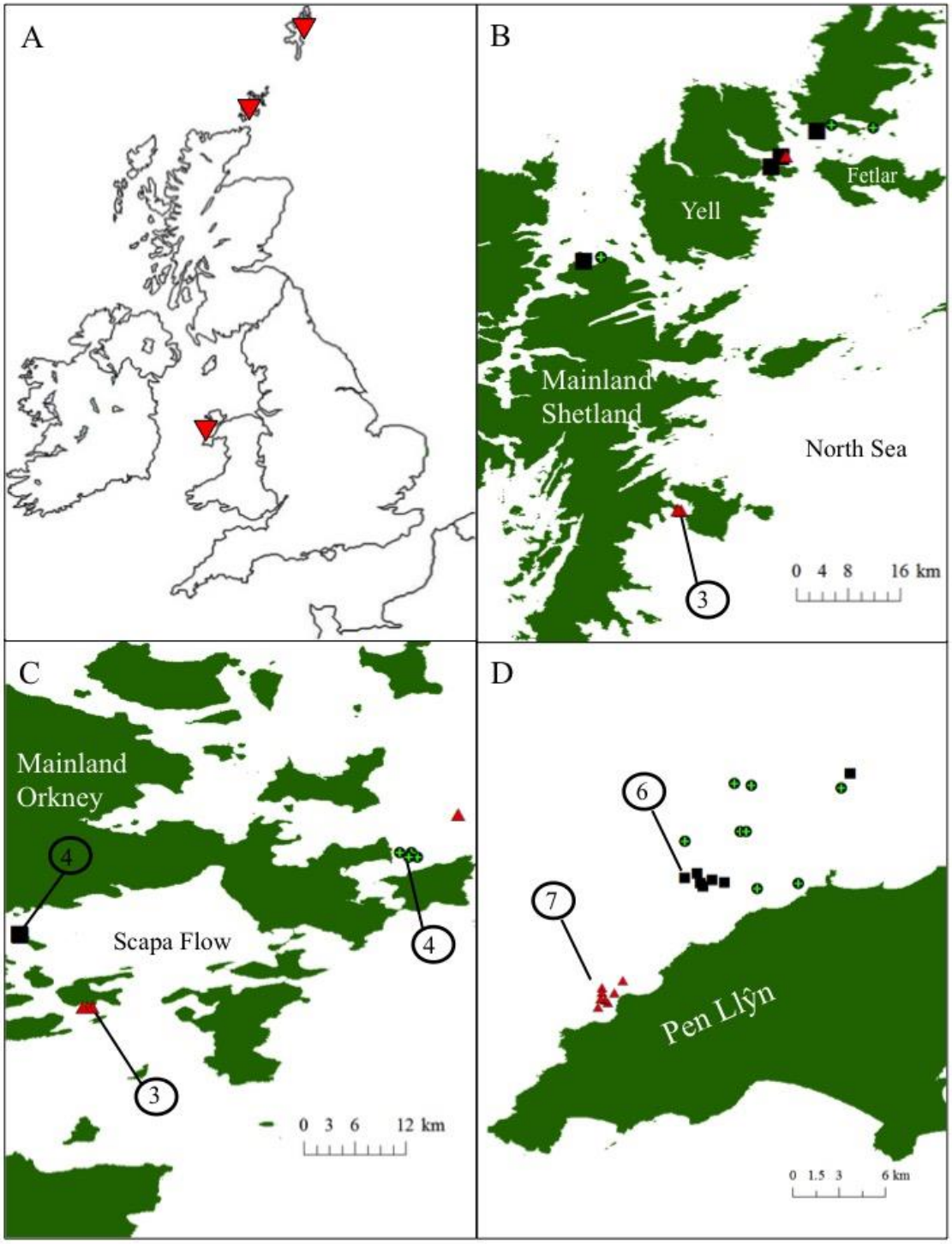

Figure 3. A) *M. modiolus* reefs study regions for megafauna abundance within the UK. B) Survey locations in Shetland (UVC method); C) Orkney (UVC method and stable isotope samples collected); and D) Pen Llŷn (Drop Down Video method). Black circle with green cross = sand habitats (16 sites in total); solid square = *M. modiolus* reefs (15 sites in total); red triangle = cobble habitats (15 sites in total). See Appendix A3 and A4 for exact locations.

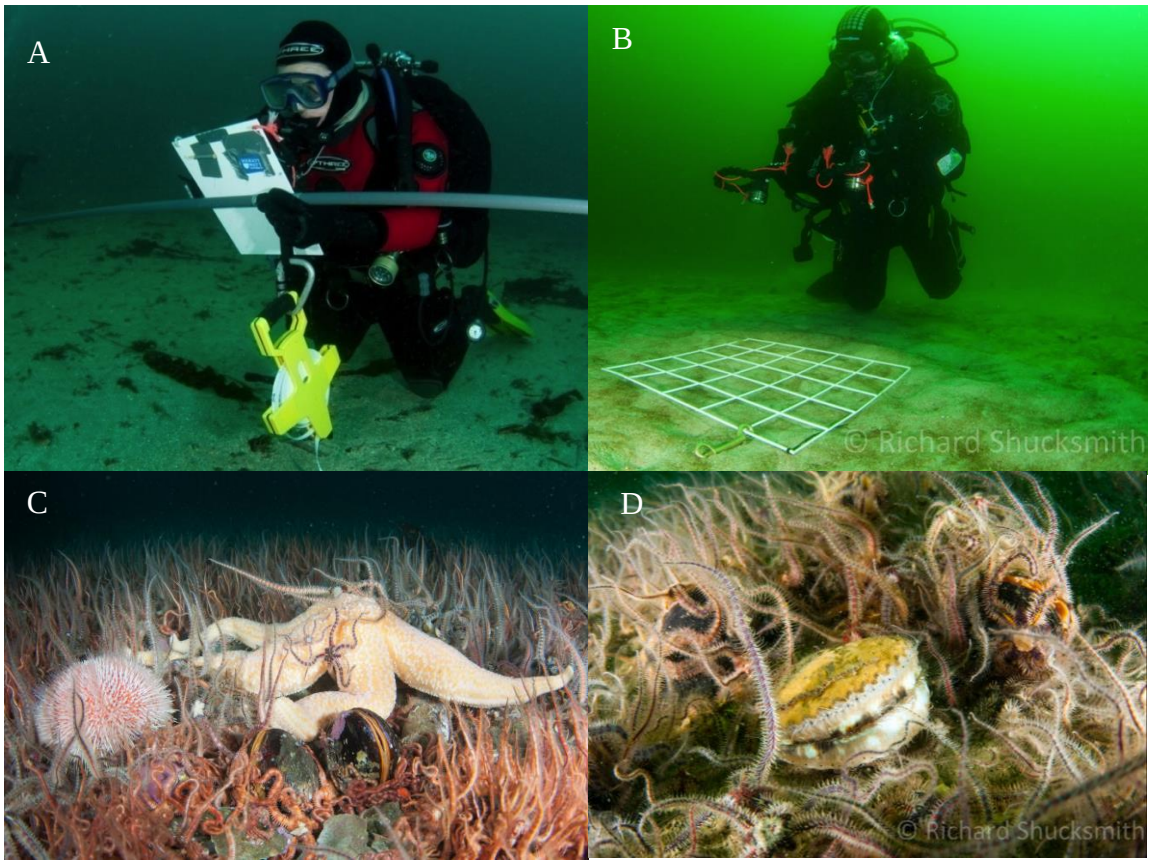

Figure 4. Divers carrying out megafaunal transects (A) and recording habitat photoquadrats (B). Megafauna species recorded on the UVC transects; *Echinus esculentus* and *Asterias rubens* (C) and *Aequipecten opercularis* (D).

At each site in Orkney and Shetland, habitat characteristics were quantified using photoquadrats which were analysed for *M. modiolus* density and percentage cover of boulders, cobbles, pebbles, shell gravel, coarse sand, fine sand and mud (see appendix A3). In order to describe the habitat in more detail, a 5cm diameter coring tube was used to take sediment samples for Particle Size Analysis (PSA) at 12 sites in Orkney. PSA samples were not collected in Shetland and habitat classification was based on habitat quadrats alone. An initial examination of the PSA samples and photoquadrats from Orkney resulted in confidence that the habitat classification for Shetland sites was correct, and photographs of the quadrats provided a good record of the site (e.g. patchiness etc.).

For the PSA, sediment samples were dried at 100°C until they reached a constant weight. Approximately 120g of each sample was mixed with sodium

hexametaphosphate (6g l^{-1}) to deflocculate the sediment (following Mair et al. 2000). The sample was stirred and left to soak for 1 hour before being sieved on a 63µm sieve. The remaining sample was dried and weighed, the difference in weight calculated as the <63µm fraction. The sample was then sieved on a sieve shaker for 15 minutes at 1 phi intervals.

A towed video camera was used to surveys sites in Wales for megafauna abundance (Figure 3D). These surveys were carried out in May and June from 2008 to 2010 and are referred to as Drop Down Video transects (DDV) for the purposes of this study. The camera system used was a Sony Model DCR-TRV950 camcorder fitted into a tubular aluminium housing. The system had two HID video lamps powered and switched from the surface unit. Removable diffusers were fitted to provide an even floodlit effect over the field of view. The video surface unit comprised a Sony GV-D1000 Digital, Mini-DV Format which included a labelling system that overlaid GPS position and depth information onto the surface image for recording and viewing.

The camera tows were intended to be 100m in length, but the exact distance was calculated from the GPS start and end points and a section of 4-8 minutes was edited from the video clip for analysis. Video footage that was too fast (>30 metres per minute) or less than 1m visibility was disregarded. The habitat was categorised as either: cobbles; *M. modiolus* reef; or sand.

Modiolus modiolus Reef Food Web Analysis - Stable Isotopes

Seventy-one samples were collected for stable isotope analysis across 3 *M. modiolus* reef sites in in Orkney. Benthic items were collected from the reefs (48 samples from 8 species). In order to sample the main carbon sources in this system, phytoplankton, macroalgae and microphytobenthos were collected. Mesoplankton were sampled throughout Scapa Flow using plankton nets (200µm mesh size). At the reef sites, benthic plankton tows were conducted by divers approximately 1m above the seabed and surface samples (~1m depth), were taken from the *MV Halton*. Drift algae and attached red algae were collected from the *M. modiolus* reefs and any epiphytes scraped off. Benthic infauna, epifauna and microphytobenthos were collected using a 'clump sample' technique where a clump of 3-5 *M. modiolus* and associated fauna are placed into a bucket along with the underlying sediment (Mair et al. 2000). Megafauna (*Asterias rubens, Aequipecten opercularis, Echinus esculentus* and *Buccinum undatum*)

were collected by swimming around the reef from a central location or on a drift dive. Fish were collected from sites adjacent to the reefs using baited creel pots.

Data Analysis

The sieved fractions from the PSA samples were standardised as a proportion of the total weight of the sample and cumulated. Multidimensional scaling ordination (based on Manhattan distance) was performed on the cumulated particle size distribution data. Manhattan distance was chosen to define the distance between samples as this is a natural measure of distance (Clarke 2006) and tends to put less emphasis on parts of the sample distributions that deviate a lot, which, in the case of sediment samples could for example be a pebble caught in the core. An analysis of similarities (ANOSIM) was used to compare the particle size distribution at the three habitat types.

For the multivariate analysis, all megafauna counts were log transformed to down-weigh very abundant species (e.g. *Echinus esculentus*, three orders of magnitude). A similarity matrix was created using Bray-Curtis similarity coefficient and an Analysis of Similarities (ANOSIM) was used to find significant differences in the megafaunal communities at the three habitat types (*M. modiolus* reef, sand and cobble). Where significant differences were found, a SIMPER analysis (Clarke 2006) was used to find the key species driving the difference in community composition. The megafaunal community composition from the DDV surveys were analysed separately from the sites surveyed using UVCs due to a difference in the methodology (Figure 5).

Counts of the three species contributing the most to the difference in megafaunal communities at the reef, cobble and sand sites were then analysed using a Kruskal-Wallis test with ‘habitat type’ as the independent variable. Where significant differences were found, pairwise Kruskal-Wallis tests were performed using a chi-squared probability distribution with a Bonferroni correction for multiple comparisons. Univariate analyses were also carried out separately for the DDV and UVC methods using R version 2.9.1.

The megafauna counts from Orkney, Shetland and the Pen Llŷn were analysed for six biological traits (see Table 2) as described by Pranovi et al. (2008). Each species was assigned to a category for each biological trait from fishbase.org and Marlin.ac.uk.

Trophic level was assigned using the $\delta^{15}N$ signature from the stable isotope analysis. The frequency of each category was calculated from the sum of the abundance of all species exhibiting that category, as a percentage of the total abundance at each site. Principle Component Analysis (PCA) was carried out on the biological traits displayed at each habitat (see Figure 5, right hand side).

Table 2 Biological traits analysed for the megafauna transects and corresponding categories. Abbreviations are used in the PCA.

Trait	**Characteristic Abbreviation**	**Characteristic Explanation**
Mobility	sed	Does not move
	slow	Moves slowly/crawls
	fast	Swims
Vertical position	benth	Benthic
	dem	Demersal
Feeding mechanism	ff	Filter feeder
	scav	Scavenger (primarily)
	pred	Predator
Longevity	Short	< 5years
	medium	5 - 10 years
	long	10-15 years
	v. long	> 15 years
Trophic Level	1	Primary consumer
	2	Secondary consumer
	3	Secondary consumer
	4	Tertiary consumer
	5	Top consumer
Size	Large	>15cm
	Small	<15cm

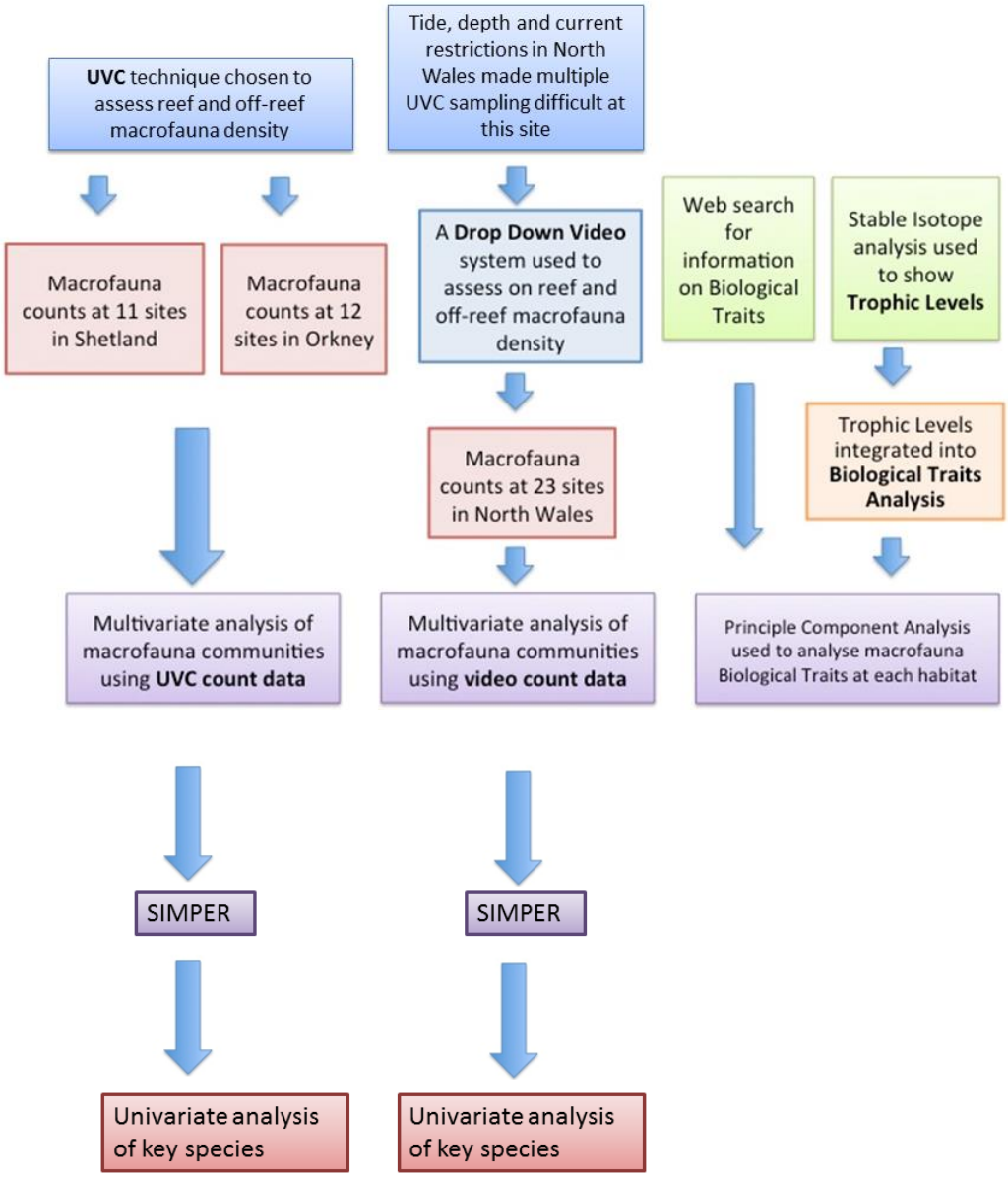

Figure 5. Flow diagram to show the methods used to assess the megafaunal communities associated with *M. modiolus* reef habitats and off-reef habitats and their functional roles.

Results

Habitat surveys

The sediment grain size distribution at the *M. modiolus* sites was significantly different to the off-reef sites (ANOSIM, p=0.001). This was because the sediment consisted of a large proportion (25%) of shell fragments (>2cm) and a large proportion (40%) of fine sand and mud (<250µm) due to the deposition of fine biodeposits (faeces and pseudofaeces) by the mussels and associated fauna. Particle size analysis showed that the sediment at the *M. modiolus* reefs sites was less variable than the sand and cobble sites (Figure 6). The PSA samples also had many small (<1 year old) gastropod shells in amongst the fine sediment.

The maximum particle size fraction measured was 3-5cm and the only sites with particle of this size were at South Flotta (Orkney). At these sites, around 50% of the particles were greater than 1.4mm and the remaining 50% of the sample was made up of medium and course sand (0.5mm – 1.4mm). The sediment at the sand sites had a very low proportion of large particles (greater than 1.4mm) and these were mainly shell fragments.

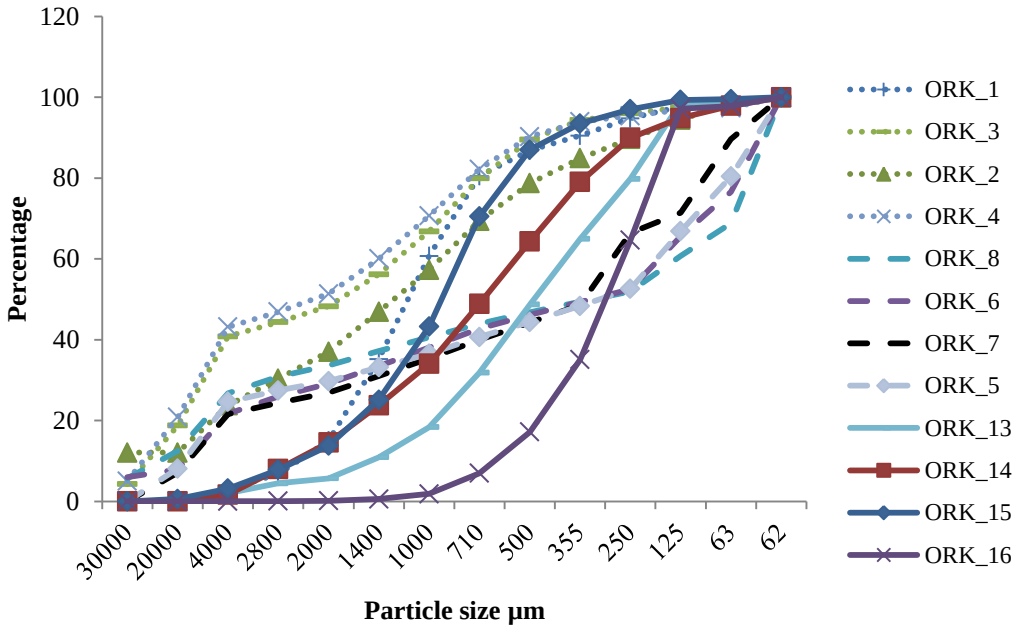

Figure 6. Cumulated particle size distribution from sediment cores at 12 sites in Orkney. Solid lines are sandy sites in Deer Sound, dashed lines are *M. modiolus* sites and dotted lines are cobble sites.

Underwater Visual Censuses – Megafauna Transects

During the 23 UVC surveys in Orkney and Shetland, 15 megafauna species were identified and counted. The megafauna community was significantly different at each habitat (ANOSIM, r=0.45, p=<0.001). Pairwise tests showed that the megafauna counted on the *M. modiolus* reefs were significantly different to those living on the sandy habitats (r=0.45, p=0.003) and the cobble habitats (r=0.38, p=0.002), as shown in Figure 7. The SIMPER analysis shows that the highest within group similarity was in the *M. modiolus* reef group (72.68%), with three species (*Echinus esculentus*, *Aequipecten opercularis* and *Buccinum undatum*) contributing 90% of the similarity. The sandy habitats were the least similar group, with an average similarity of 20%. The high counts of flatfish and dragonets at sandy sites contributed 70% of the similarity within the sandy sites.

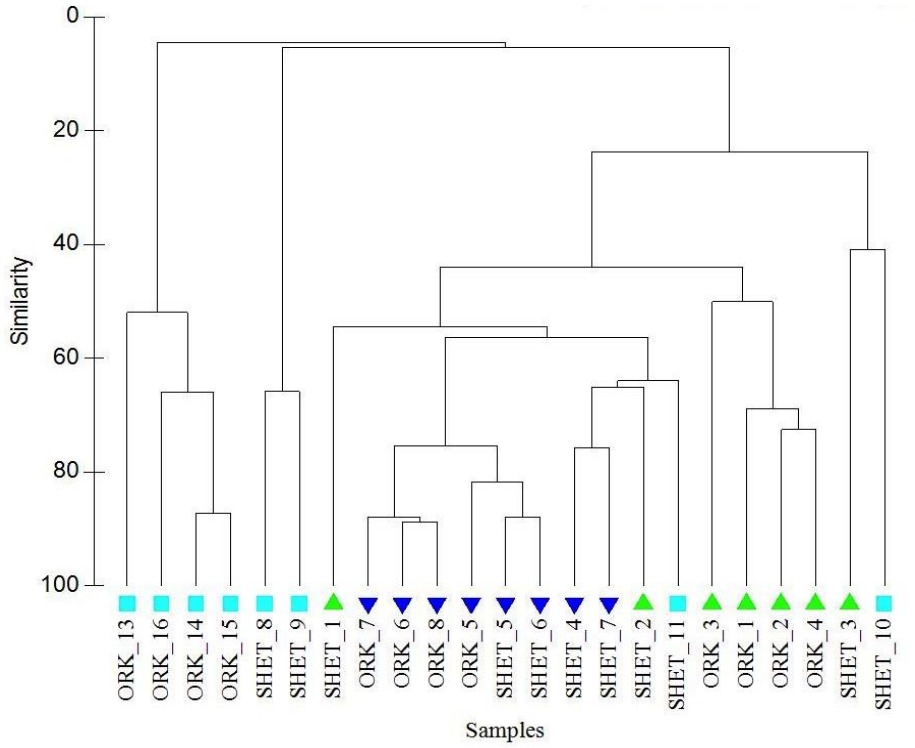

Figure 7. Dendrogram of megafauna counts at transects in Orkney and Shetland using Bray-Curtis similarities calculated on log transformed data. Symbols represent habitat type: Green triangles = cobble habitats; blue squares = sandy habitats; inverted blue triangle = *M. modiolus* reef habitats.

The *M. modiolus* reef sites were most dissimilar to the sandy sites (90.41% dissimilarity) and this is largely due to the difference in invertebrates and fish counts at these sites. *M. modiolus* reef sites had over 5 times more *A. opercularis* per transect than the cobble sites (X^2 =11.011, p=0.001) and more than 20 times as many as the sand sites (X^2 = 12.427, p=<0.001). *B. undatum* were also more than 5 times as abundant on the reefs than cobble sites and almost twenty times more abundant than sand sites (X^2 = 7.136, p=0.008). However, the counts at the reef were not significantly different to the cobble sites at the 0.05 significance level (X^2 = 3.84, p=0.050). The most abundant species found on the *M. modiolus* reefs was *E. esculentus* (0.46 per m^2), which was significantly greater than the cobble sites (X^2 = 9.442, p=0.002) and the sand sites (X^2 =12.308, p=<0.001).

On the UVC transects, gobies (*Pomatoschistus pictus* and *Pomatoschistus microps*) were abundant in all habitats, but especially the sand sites (a maximum of 24 *P. pictus* counted on one transect). Juvenile flatfish (*Limanda limanda*) were abundant at two of the sand sites and dragonets (*Callionymus spp.*) were present at three out of eight sand sites (16 counted in total). The fish species associated with the *M. modiolus* sites were different to those associated with the sand sites. For example *Diplecogaster bimaculata* occurred at the *M. modiolus* sites but not at the off-reef sites.

Drop Down Video Transects - Megafauna Transects

A total of 23 megafauna species were identified from the DDV analysis at 24 sites on the Pen Llŷn, North Wales (see Figure 3 for sampling locations). The megafaunal community associated with the *M. modiolus* reef were significantly different to the sand and cobble habitats (ANOSIM, r=0.26, p=<0.001). The top three species highlighted in the SIMPER analysis as causing the difference in community structure between *M. modiolus* reef sites and off-reef sites were (in order of importance) *B. undatum, Asterias rubens,* and *Maja brachydactyla,* previously known as *Maja squinado* (Sotelo et al. 2007). The cumulative contribution of these three species in the difference between habitats was 44.15% between reef and sand habitats, and 44.72% between reef and cobble habitats. Other key species causing differences in the species assemblages were *Eledone cirrhosa* and *E. esculentus.*

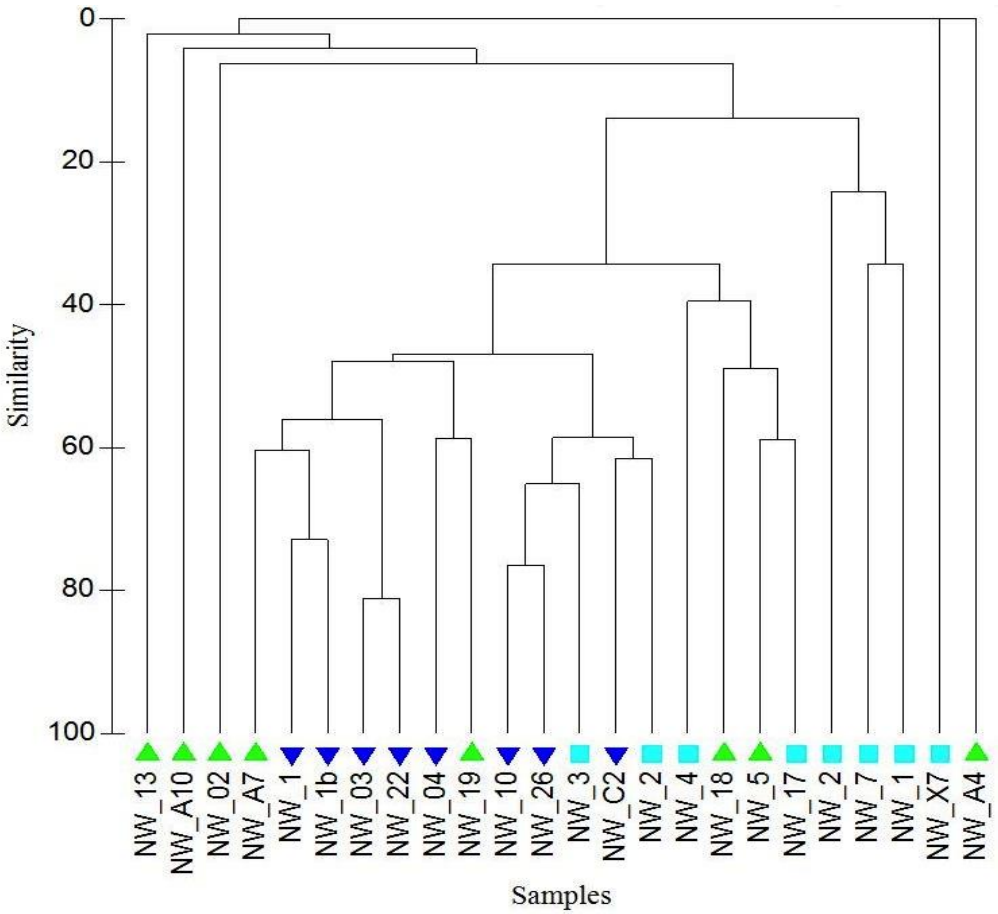

Figure 8. Dendrogram of megafauna counts at DDV sites in Wales using Bray-Curtis similarities calculated on log transformed megafauna abundance data. Symbols represent habitat type: Green triangles = cobble habitats*;* blue squares = sandy habitats; inverted blue triangle = *M. modiolus* reef sites.

As with the UVC megafauna data, the *M. modiolus* reef group had the highest within group similarity (52.54% compared to 24.27% for sandy habitats and 14.49% for the cobble habitats). The most common fish species associated with the *M. modiolus* reef was *P. gunnellus* which contributed 8.67% towards the within group similarity at the *M. modiolus* sites. The off-reef sites had different fish associated with them, for example, wrasse (*Labrus bergylta*) on the cobble sites and dragonets (*Callionymus spp.*) on the sand sites.

The DDV transects showed that *A. rubens* was the most abundant species and there were significantly more observed on the reef than the sand ($X^2 = 9.26$, p=<0.001) and cobble habitats ($X^2 = 11.618$, p=0.002). From the DDV analysis, no *B. undatum* were identified on cobble sites, although they were occasionally seen on the reef and sand

sites. *Maja brachydactyla* were more abundant at the reef sites (0.01 per m^2 on average) than the cobble (0.002 per m^2) and sand sites (0.002 per m^2) although this was not significant (see appendix A7). Ballan wrasse (*Labrus bergylta*) occurred on the cobble sites but not on the sand sites, however, goldsinny wrasse (*Ctenolabrus rupestris*) were observed at both the cobble sites and the sandy sites. Sea scorpions occurred at the reef sites and the cobble sites but not on the sandy sites, whereas dogfish (*Scyliorhinus canicula*) occurred on the reef sites and the sand sites but not the cobble sites. The butterfish (*P. gunnellus*) and octopus (*E. cirrhosa*) only occurred on the *M. modiolus* reef and were not seen on any other habitat.

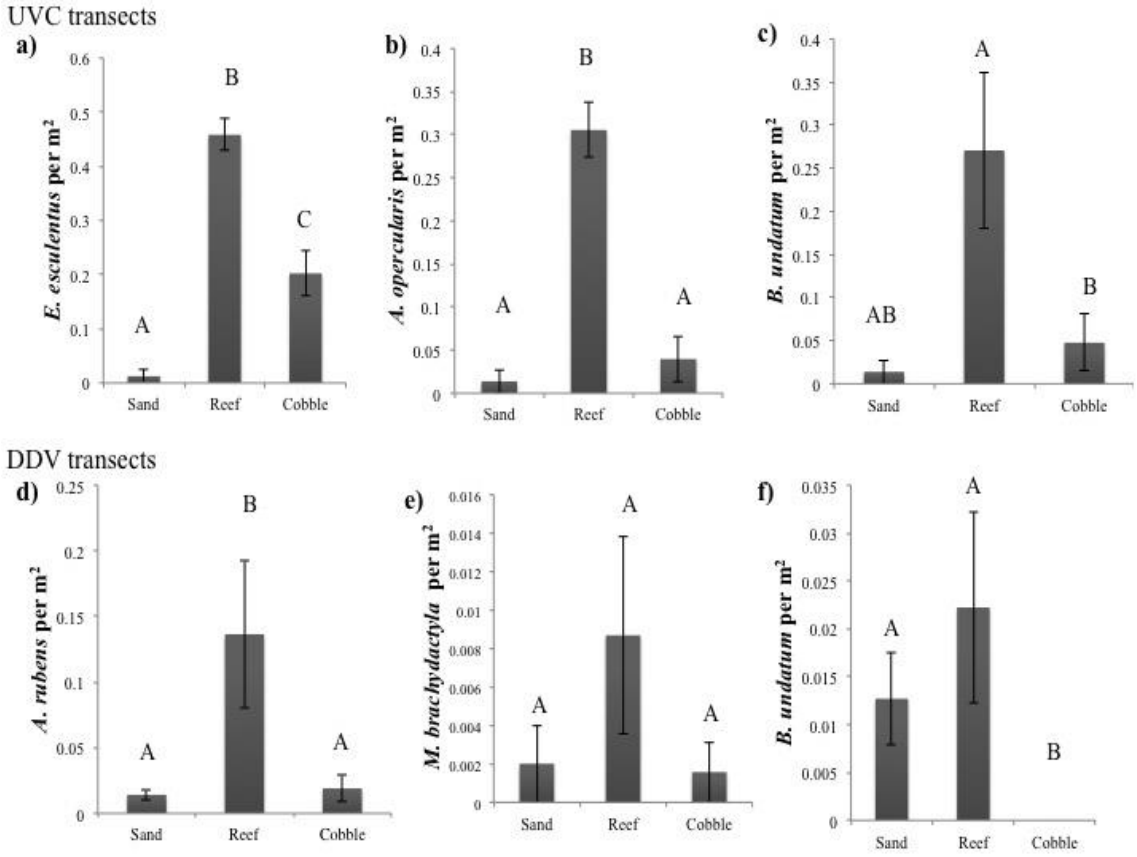

Figure 9. Average counts of key species highlighted by the SIMPER analysis ±1 SE in the Underwater Visual Censuses counts (a-c) and Drop Down Video Transects (d-e). Groups that share a capital letter are not significantly different (Kruskal Wallis test). Pairwise comparisons are shown in Appendix A6 and A7.

Foodweb Analysis

The *M. modiolus*, *A. opercularis*, and *B. undatum* samples from Orkney showed consistent stable isotope signatures (Figure 10). Even *M. modiolus* samples from different reefs (up to 2km apart) showed very similar $\delta^{13}C$ and $\delta^{15}N$ values, suggesting that the site is not important at this scale. The highest $\delta^{15}N$ values were from the fish samples, which implies that these animals are at the top of the food chain for the organisms samples in this system, and possibly feeding on crustaceans and bivalves on the reef. The isotope ratios from *M. modiolus* and *Aequipecten opercularis* samples formed two distinct groups (Figure 10), which indicates that these two species selectively feed on different parts of the plankton. The Nitrogen ratio is a good indicator of trophic level, with an increase of 3‰ equivalent to approximately one trophic level. For example, the average $\delta^{15}N$ for *M. modiolus* is 9.21‰ compared with 11.67‰ for whelks (*B. undatum*), implying that whelks are one trophic level higher than *M. modiolus.*

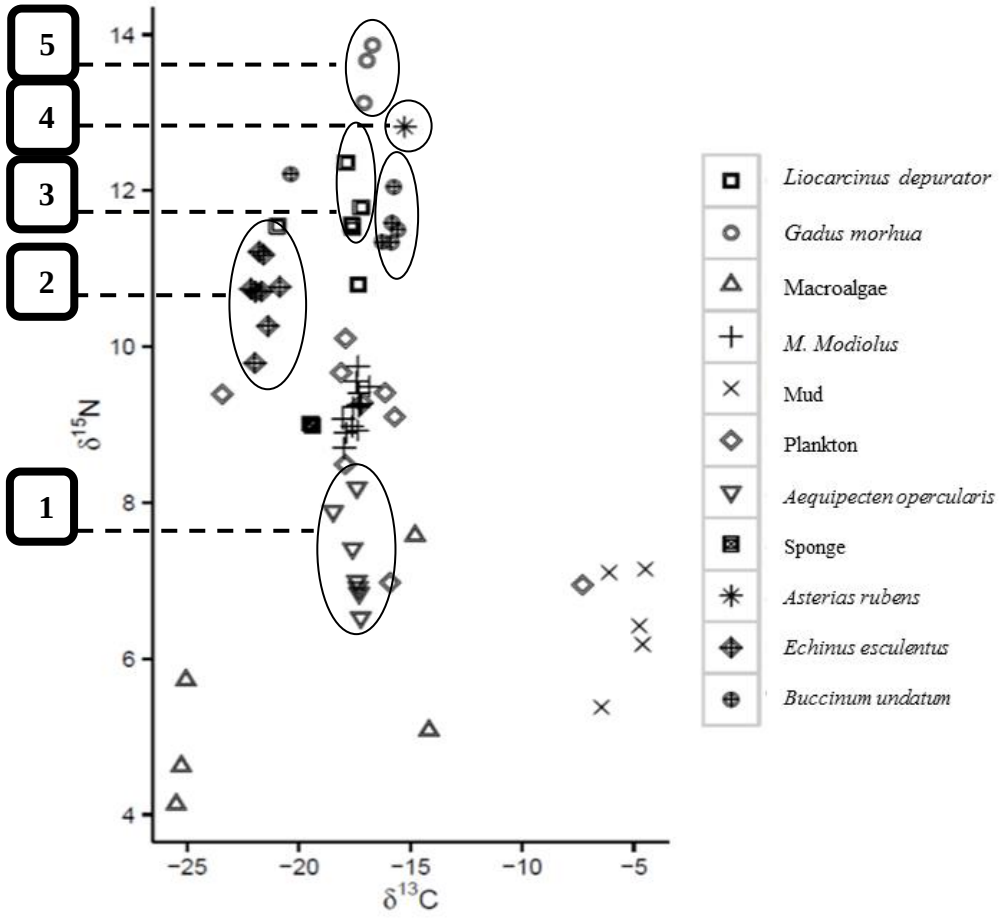

Figure 10. Stable isotope analysis of the *M. modiolus* reef community in Scapa Flow, Orkney, with the key megafauna consumer species associated with the reef in the food chain highlighted 1-5 as increasing trophic steps.

The mud samples collected to analyse the microphytobethos show $\delta^{13}C$ values approximately -5‰ which suggests that these have a high concentration of carbonate in them. This is not surprising considering that the benthic sediment is largely made up of *M. modiolus* shell material. However, the mud samples are not accurately representing the primary production from benthic phytoplankton. The average percentage of Carbon in the mud samples was 10.87%.

Biological Traits Analysis

The PCA results indicate that the megafauna associated with the sandy habitats form a group according to their biological traits (Figure 11). This group is characterised by highly mobile demersal fish at the highest level of the food chain. Typical species with these characteristics that occurred in the sandy habitats were dragonets and flatfish. Sandy sites also had high counts of short-lived species (less than 4.5 years), such as the painted goby (*Pomatoschistus pictus*). See appendix A8 for biological traits assigned to each species.

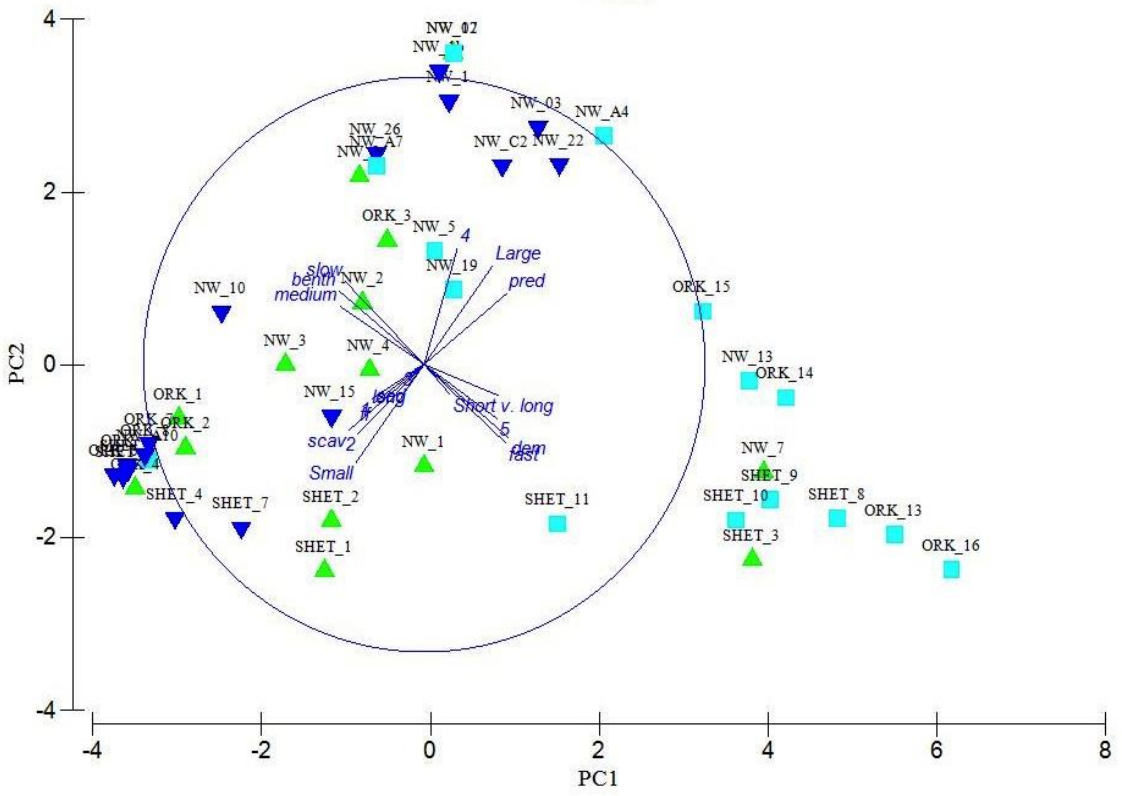

Figure 11. Principle component analysis of the proportion of biological traits displayed at each site by the megafauna communities surveyed using UVCs and DDV transects. Blue squares = sandy habitats, green triangles = cobble habitats; and inverted blue triangle = *M. modiolus* reef habitats.

Less mobile, benthic species with a medium lifespan characterised the cobble and reef habitats. The reef sites formed two distinct groups with regards to the biological function of the megafauna. Species associated with the Pen Llŷn reef transects were often large predators, whereas the fauna that were counted on the reefs in Orkney and Shetland were smaller and feeding at a lower trophic level in general. Filter feeders such as *A. opercularis* and scavengers, such as *E. esculentus* were particularly abundant on the reef sites in Orkney.

Discussion

This study shows that the key megafaunal species associated with *M. modiolus* reefs are *A. opercularis, E. esculentus, A. rubens* and *B. undatum.* Both the UVCs and the DDV surveys showed that *M. modiolus* reefs have a greater abundance of shellfish associated with them than the off-reef sites. *M. modiolus* reefs are recognised for their conservation importance and protected in Special Areas of Conservation under the EC Habitats Directive. The objective of the Habitats Directive is to conserve biodiversity (McLeod et al. 2009), however, the evidence given here shows that *M. modiolus* reefs support commercially important species and therefore protection of these habitats may have additional fisheries benefits.

The two methods used in this study (UVCs and DDV) provide a comprehensive and relatively non-biased method for measuring megafauna abundance; a wide range of species were sampled and the area of seabed sampled could be easily defined. The benefit of the UVC technique was that the diver was able to look around objects to check for conspicuous species, however, the DDV technique covered a larger area of the seabed and the species identity could be checked by pausing the video and using reference material.

As indicated by Bozec et al. (2011), it is likely that cryptic fish species are underrepresented in the more complex habitats using these visual transect methods. Also, low mobility species could have been missed at the reef sites, especially using the drop down video technique. For example, *Pecten maximus* and *B. undatum* are likely to be missed from records on the *M. modiolus* reefs because they remain stationary and are

a similar colour to the surrounding habitat, whereas *A. opercularis* swims away when disturbed thereby more easily spotted on a dive transect or in a video.

Larger mobile species of fish were rarely spotted on the UVC transects, perhaps due to the presence of the divers and bubbles deterring them (Schmidt and Gassner 2006), although few large fish were seen on the DDV transects either, and those that did occur were often on the cobble habitats. All habitats surveyed were located in areas exposed to high current velocities, therefore it may be the case that for a highly mobile fish species, the energetic cost of maintaining a position in the water column at these sites was not viable, as shown by Rosenfeld and Boss (2001). Large boulders seen occasionally at the cobble sites may provide some protection from the strong currents, for mobile species.

The biological traits analysis shows that the species assemblages associated with the different habitats perform different ecosystem functions. It has been shown that in highly diverse ecosystems, species can become redundant if they are performing the same functions as others in the system (Dumay et al. 2004). Therefore, prioritising habitats for conservation should take into account the 'originality' of species (Pavoine et al. 2005). This concept suggests that rather than studying biodiversity in a system, it is more useful to study biological traits in order to determine which species are more 'original', that is, species that have a greater proportion of rare features, compared to species that carry out many similar functions to others in the community. In the context of the present study, analysis of the biological traits of the megafaunal communities studied shows that the Pen Llŷn reef supports a wider range of functional groups than the Orkney and Shetland reefs. However, the three different habitat types support a greater range of functional traits still, suggesting that habitat heterogeneity is important for maintaining ecosystem function in a wider sense.

Interestingly, the Pen Llŷn reef supports megafauna that are functionally different from those on the reefs in Orkney and Shetland. This could be partly due to the difference in method used (although this separation is not so pronounced with the other habitats) with sedentary species being more difficult to see on the video. However, this reef is also in a different environmental setting as it is on an exposed part of the coastline and very dense in places (Rees et al. 2008).

The stable isotope study gives an insight into the structure of the reef food web, for example the isotopic values of *B. undatum* suggest that they are feeding on *M. modiolus.* This supports evidence we already have from the megafauna counts that *M. modiolus* reefs are an important habitat for *B. undatum*. Predation on bivalves by *B. undatum* has been observed in a laboratory setting (Scolding et al. 2007), which means that they could be feeding on *M. modiolus* and other bivalves directly. Also, the presence of small gastropod shells in the sediment samples taken from the reef sites indicates that species such as *B. undatum* bury themselves in the sediment after they hatch from the egg capsules, possibly as a predator protection mechanism, suggesting that the surveys described here may have underestimated their presence.

The stable isotope data also shows the range of feeding mechanisms on the reef and the different food sources on the reef available for mobile species. The tissue samples from *M. modiolus* and *A. opercularis* adductor muscles show two distinct groups, with *M. modiolus* feeding at a slightly higher trophic level. This would explain why the two filter feeding species can live successfully and in high densities in the same location, as they are likely to be feeding on different fractions of the plankton. Selective feeding is a contentious issue in the bivalve feeding literature, however, there is an increasing amount of evidence that builds the case for different shellfish species having the ability to select for different particles in suspension (Shumway et al. 1985, Kiorboe and Mohlenberg 1981, Ward and Shumway 2004). This suggests that *A. opercularis* and *M. modiolus* may have separated feeding niches.

There are limitations with the stable isotope study because sample sizes are small and there was a lack of pre-treatment on some of the samples. For example, C:N ratios of around 7 in *E. esculentus* are probably attributable to the high lipid content which is depleted in ^{13}C in the tissues analysed for this species. To counter this bias, extraction of this lipid prior to analysis is suggested, though this process can have a significant and unpredictable effect on the $\delta^{15}N$ (Post et al. 2007).

The isotope results from the plankton samples were highly variable and were likely to be a mixture of phytoplankton and zooplankton. The samples were washed with distilled water but it is possible that they still had some salt particles in them, which could have affected the results. In future studies, separation of the plankton into multiple size fractions would give a good indication of the diet of different species on a

M. modiolus reef and perhaps provide further evidence for selective feeding on different sized organisms by *M. modiolus* and *A. opercularis.*

The microphytobenthos samples taken from the benthic sediment showed $\delta^{13}C$ values approaching that of marine carbonate and a high C:N ratio, suggesting a high proportion of shell material in the samples. PSA of sediments from *M. modiolus* reef sites in the UVC surveys showed a high proportion of very fine sand and silt, with large shell. This has also been reported by Nic Aonghua et al. (2001), who found that the carbonate content of the sediment was up to 60% of the sediment in areas of dead shell and a high organic content of sediments in the dense living parts of the reef. This organic material may provide an important source of food for megafauna living on the reefs and the high carbonate content within the reefs is important for carbon sequestration as the reef develops (Burrows et al. 2014).

The key commercially important species associated with *M. modiolus* reefs were *B. undatum* and *A. opercularis*. *B. undatum* could be feeding on the mussels and associated fauna, whereas *A. opercularis* are more likely to be using the complex reef habitat as an attachment site during the early life stages. Spider crabs (*Maja brachydactyla*) were also abundant on the Pen Llŷn *M. modiolus* reef compared to the off-reef sites and this species is harvested throughout the Europe, especially in the English Channel and the Mediterranean (Fahy 2001). Within the UK, *Maja brachydactyla* is largely distributed on the south coast of England and Wales; however, its distribution may extend further north with rising seawater temperatures (Goodwin et al. 2013). *B. undatum* are fished across the UK and is an important inshore fishery (Shelmerdine et al. 2007). Although catch rates of *A. opercularis* have fluctuated over the past 30 years, they are also of economic importance in the UK (Beukers-Stewart and Beukers-Stewart 2009).

Complex biogenic habitats such as oyster reefs and Maerl beds have been shown to support a high biomass of commercially important fish and shellfish species (Kamenos et al. 2004c, Kellogg et al. 2011). The evidence provided here suggests that *M. modiolus* are of a similar value to commercial fisheries in their role as an essential habitat. As with maerl beds, *M. modiolus* reefs are sensitive to physical impact (Hall-Spencer and Moore 2000, Cook et al. 2013), and a loss of these supporting habitats will have implications for the shellfish populations that rely on them.

Chapter 3. The functional role of a horse mussel (*Modiolus modiolus*) reef as a habitat for the common whelk, *Buccinum undatum.*

Abstract

The Pen Llŷn horse mussel (*Modiolus modiolus*) reef complex constitutes two beds, which cover a total of 600 hectares. The reef area in this study has been closed to mobile fishing activity since November 2012, however, the use of static gear is permitted and common whelks (*Buccinum undatum*) have been harvested from this area for the past 25 years. By working with local fishermen data were collected on whelk catch rates and size distributions at stations on and off the reef using baited pots. *B. undatum* catches were three times higher on the *M. modiolus* reef. High catch rates of small (<6cm) whelks on the reef suggests that this is a nursery habitat for whelks and sustains the local pot fishing activity. Understanding the functional role of biogenic habitats such as horse mussel reefs, and the benefits that they can provide to local communities, can make an important contribution to conservation management.

Introduction

The common whelk, *B. undatum*, is among the top three most valuable shellfish species caught in Wales with landings of 5000 tonnes in 2013, worth £3.6 million (MMO, 2014). The Pen Llŷn is a remote location and the whelk fishery supports 12 fishers working four vessels from Porth Dinllean. Fishing occurs over two horse mussel reefs and each vessel collects approximately 150 tons of whelk each year. *M. modiolus* reefs are made up of a diverse array of infaunal and epifaunal species associated with the mussels (Rees et al. 2008, Sanderson et al. 2008), and therefore could potentially provide an important source of food for fish and shellfish.

B. undatum are a common subtidal species, harvested throughout the UK using baited pots (Shelmerdine 2007). *B. undatum* are well adapted to detect dead animals on the seabed to feed on, however evidence suggests that they are also active predators, feeding on polychaetes and bivalves (Himmelman and Hamel 1993). It has been

reported that *B. undatum* attack bivalves by inserting the lip of their shell in between the two valves and extracting the bivalve flesh using an extendible proboscis (Hancock 1960). An alternative feeding method is described by Scolding et al. (2007) and involves the whelks using their foot to asphyxiate cockles (*Cerastoderma edule*) or to pull the cockle's valves apart.

Breeding occurs in autumn and winter and the whelks lay large egg masses on the seabed. Each egg capsule within the egg mass contains around 2700 eggs which are vulnerable to predation. Martel et al. (1986) found that a single egg mass from one female *B. undatum* can produce approximately 3700 juveniles. The lifecycle of *B. undatum* is entirely benthic and lacks a planktonic stage (Valentinsson et al. 1999). This is likely to result in local populations with reduced gene flow and spatial differences in morphological traits, which makes the populations vulnerable to over exploitation (Valentinsson et al. 1999). However, Martel et al. (1986) report a high rate of polygamy, and multiple fertilisations at one egg laying location could be an important mechanism to increase genetic variability in low mobility species.

Marine resources are increasingly being managed with respect to the rest of the ecosystem. The term 'ecosystem approach' became formally accepted in 1992 as part of the Convention on Biological Diversity and has become a fundamental part of fisheries management. In 1996, the United States made amendments to the Sustainable Fisheries Act (SFA) and required all fisheries management councils to identify the 'Essential Fish Habitat' (EFH) for commercially important fish species (Fluharty 2000). This approach aims to identify, conserve and restore fish habitat in order to sustain healthy fish stocks.

Effective management of marine habitats requires prioritisation of areas of the seabed that are important at critical stages of development (Mangel et al. 2006). Able (1999) suggests four levels of assessment to determine whether a habitat is essential for a particular species: Level 1) presence/absence, level 2) relative abundance, level 3) relative growth, survival or reproduction rates, level 4) relative productivity.

The aim of this experiment is to find out if the Pen Llŷn *M. modiolus* reef is an EFH for *B. undatum*. The experiment will test the hypotheses that 1) there is a greater abundance of whelks on the horse mussel reef compared to other areas of the seabed; and 2) the whelks on the reef have a different size structure and growth rate to those caught on

'off-reef' habitats. In addition, the hypothesis that *B. undatum* will actively favour *M. modiolus* reefs over control sites if displaced was tested with mark and recapture experiments.

Methods

Study site

For the past 25 years up to five fishing boats have harvested common whelks (*Buccinum undatum*) using baited pots on the north coast of the Pen Llŷn in Wales and fishing follows a systematic pattern, moving along the coast in a north-easterly direction from February to September each year. The total reef area is approximately 600 ha; the southern part of the reef has been mapped and monitored since 1999 (Lindenbaum et al. 2008) and the second smaller section of reef to the north of Porth Dinllean was first recorded in 2010 (Lindenbaum pers. com.). The southern reef is part of the Pen Llŷn a'r Sarnau Special Area of Conservation (SAC) and has been closed to mobile fishing activity since 1998, and the northern reef was closed in 2012 (Figure 12). During the scallop dredging season (November – April), the pot fishermen are restricted to fishing on the reefs, inside the closed areas, because pots can be lost when snagged by the mobile fishing gear (P. Jones pers. comm. 2013).

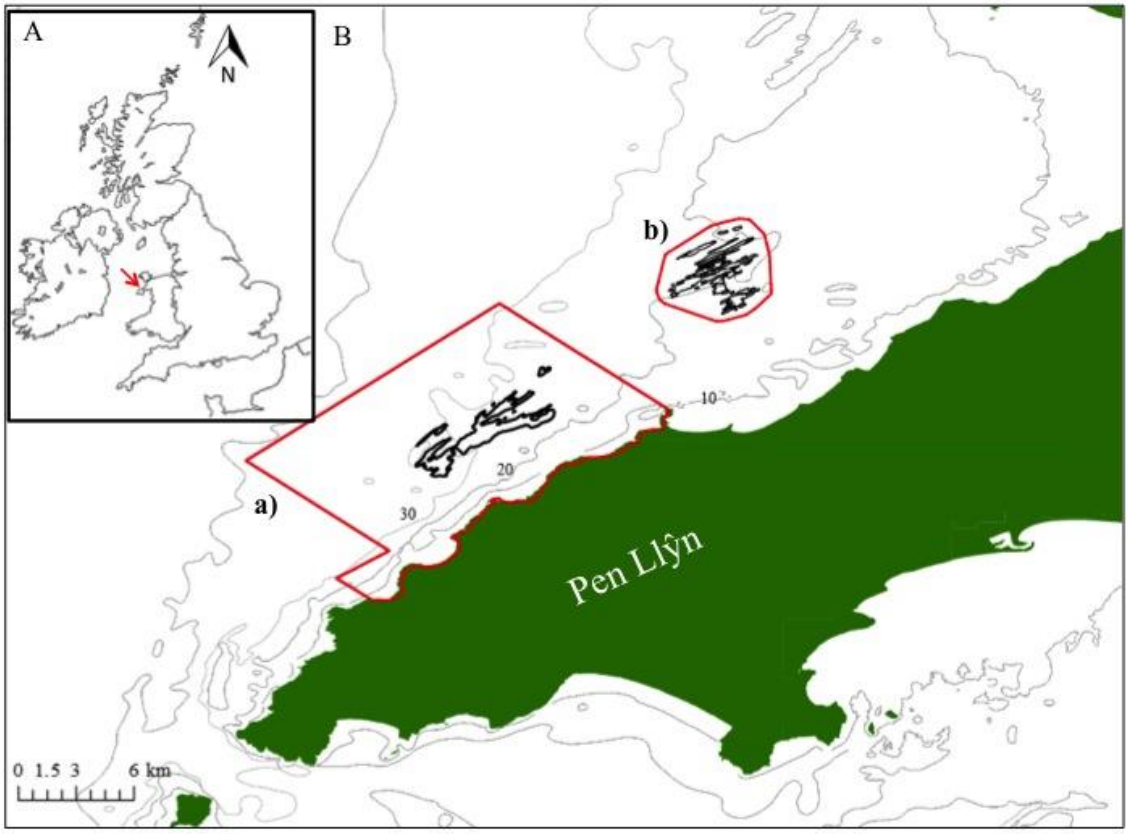

Figure 12. A) The location of the Pen Llŷn *Modiolus modiolus* reef complex in the UK. B) The two *M. modiolus* reefs to the north of the Pen Llŷn. Reef outline (solid black line), created using side scan sonar (Lindenbaum et al. 2008; Lindenbaum unpub. data). The red lines show the two areas closed to mobile fishing gear (a and b).

Whelk abundance was assessed in June and July 2013. Baited pots were deployed at 61 sites off the Pen Llŷn, North Wales (19m – 30m below chart datum) on the *M. modiolus* reef and adjacent areas (Figure 13). Sites were selected by creating a grid in GIS and using the 'Create Fishnet' tool to randomly select positions on the grid. Some of the selected sites were logistically impractical to access and were therefore moved to the nearest point on the fishing route. Control sites were selected in areas to the south (n=14), north (n=15) and east (n=15) of the horse mussel reef (n=17) to accommodate any variation that might have occurred as a result of bathymetry or tidal flow. Drop down video footage was used to confirm the habitat at the reef sites and four control areas. The control areas were approximately 3km from the reef. The more northern reef (Figure 12 'b') was used in this study to synchronise with the fishing schedule.

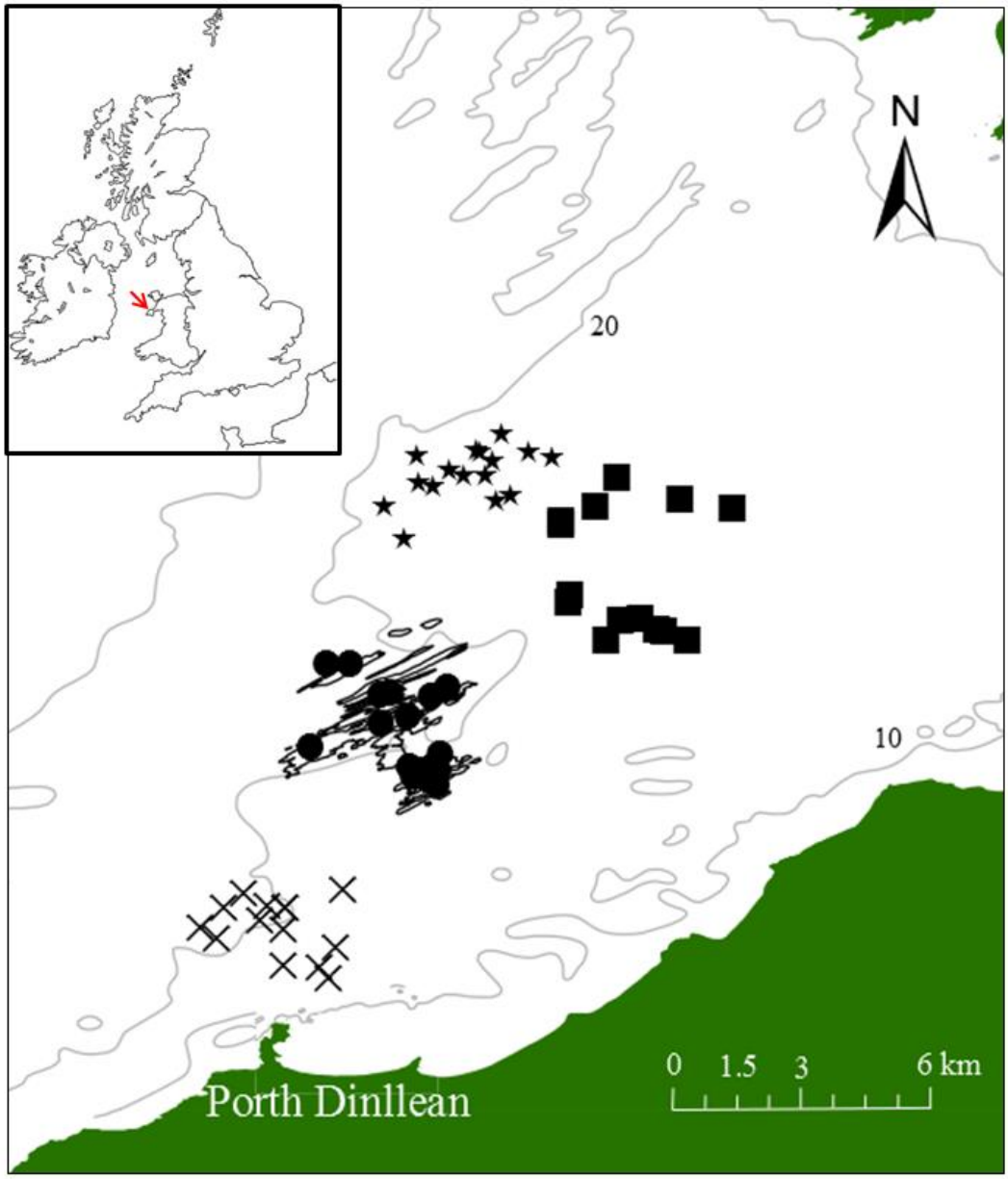

Figure 13. Sampling locations: Stars = North Control Area; squares = East Control Area; circles = Reef; crosses = South Control Area. Tag-release sites shown: green triangle = black tag, red circle = coloured tags, white circle = white tags. Reef outline shown in black.

The fishing gear was made from 25 litre plastic drums with concrete at the bottom and a hole in the top covered in net material with a simple draw-string opening. They were deployed in strings of 20 pots and one pot from the string was selected at random at each site to remove any catch rate variation along the string. The bait used was half a dogfish (*Scyliorhinus canicula)* and half a spider crab (*Maja brachydactyla*) and the gear was left overnight for 24 hours. This technique was chosen because it is the

industry standard method for catching whelks. The *B. undatum* in each pot were counted and measured (maximum length).

Age Determination - Growth Rate

Population structures in whelks were determined by age assessment whereby the opercula were removed from animals at 4 sites for growth rate analysis. Samples were from the North Control area (n=71), the reef (n=153), the South Control Area (n=92) and the East Control Area (n=61). Counting rings on *B. undatum* opercula to estimate growth has been shown to be comparable to other methods such as length frequency analysis (Kideys 1997). The operula were cleaned using ethanol and the age rings on the underside of the opercula (Figure 14 A) were counted under a dissection microscope following Ilano et al. (2004) where 1 ring shows 1 year of growth. A section of each operculum was taken from the centre where the smallest age ring was found, to the outer edge. The sectioned opercula were then mounted and the number of striae within each operculum counted to verify the initial counts (Figure 14 B). Only opercula with clear striae were used for analysis.

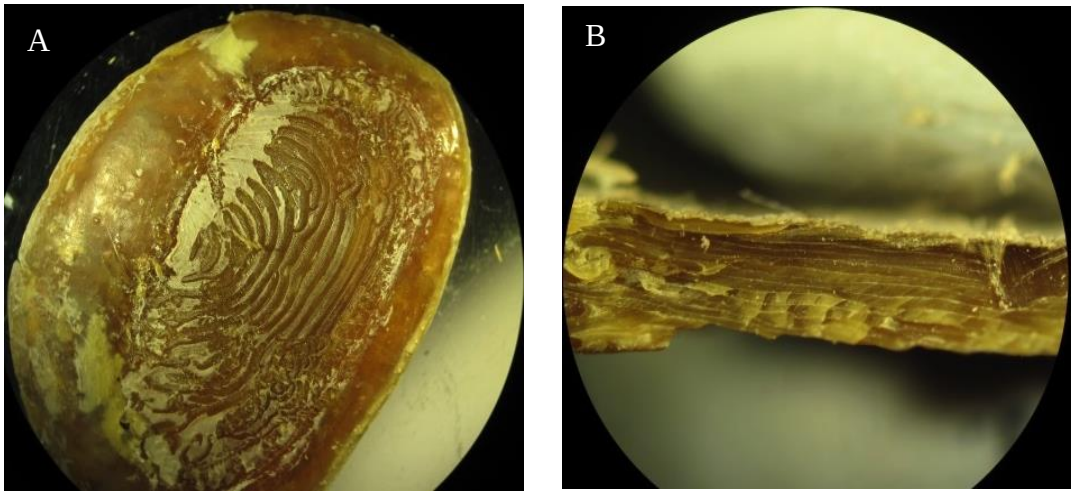

Figure 14. An example of a *Buccinum undatum* operculum showing A) the underside of the operculum where the foot attaches and B) a cross section of the operculum from a 12 year old.

Migration

In order to find out if *B. undatum* move between areas a tagging experiment was trialled in June 2013 using paint following Henry and Jarne (2007); however, this resulted in a high mortality rate, so an alternative method was developed in July 2013. The most effective tagging technique used was to attach a cable tie around the largest whorl of the shell. The tagged whelks were taken from a single pot and released in the same location that they were caught from. Black tagged whelks were released on the reef, white tags were used on whelks released to the north of the reef and coloured tags were used on the whelks released at the East Control site (Figure 13).

Data Analysis

Counts of *Buccinum undatum* were converted to catch rate (number of *B. undatum* per pot for each 24 hour deployment). *B. undatum* count data were not normally distributed, therefore the counts were square root transformed and an Anderson-Darling test was used to test for normality. The data were tested for equal variance (Levene's test), and the transformed count data at the 4 areas (1 on reef and 3 off-reef areas) were compared using an analysis of variance (ANOVA). A Tukey multiple comparisons test was used to further explore these differences. A linear model was used to examine the relationship between transformed *B. undatum* counts and depth. All univariate analyses were carried out in R version 2.9.1 (R Development Core Team 2011).

In order to test the difference in size distribution of *B. undatum* from the different areas, analysis was carried out using the PRIMER v6 statistical package with PERMANOVA + add-on (Anderson et al. 2008). The four areas tested are shown in Figure 13; these areas are the *M. modiolus* reef and the three control areas (to the north, east and south of the reef).

Multidimensional scaling ordination (based on Manhattan distance) was used to visualise the cumulated *B. undatum* size distribution data. A two-way design was created with 'area' as a fixed factor and 'depth' as a random factor nested within 'area' (therefore removing any confounding influence of habitat and depth (Anderson et al. 2008)). The model was tested using a permutation analysis of variance (PERMANOVA). Data collection in the field resulted in an unbalanced design which was therefore tested using Type III sums of squares as with this approach, every term in

the model is fitted after taking into account all other terms in the model (Anderson et al. 2008). Where significant differences were found, pairwise tests between the groups were used to find where these differences occurred.

Growth rates of *B. undatum* were calculated according to mean length per age class and determined according to the von Bertalanffy growth formula (VBG), $Lt=L\infty(1-e^{-k(t-t_0)})$, where Lt=length at a given age, L∞=maximum length, k=rate constant, t=age, and t0=theoretical age at length 0. *B. undatum* growth curves were compared for those caught in the three areas using the likelihood ratio test (Kimura 1980) and the "FSA" statistical package in R (Ogle 2013b). VBG models for each area were compared to a 'typical' model using the entire data set following the Von Bertalanffy Growth Models vignette (Ogle 2013a).

Results

Overall, 3913 whelks were caught in 61 pots off the Pen Llŷn and of these, 2037 were from the reef. There were significantly more whelks caught at the reef site than any of the control sites (ANOVA, F = 11.09, p=<0.005), see Figure 15. There was a large spatial variation in catch rates within areas, especially at the South Control area. For example, 183 whelks were caught at site 97 and 400 metres away, only 1 whelk was caught at site 98. Catch rates on the reef were consistently high, and the highest catch occurred on the reef, with 320 whelks in one pot. The lowest catch rates were at the South Control area with fewer than 5 whelks caught at 4 sites. Whelks caught at the reef site had some morphological differences also; their shells were often more brittle and had epifauna growing on them (e.g. hydroids), whereas whelks caught at the control sites were clean.

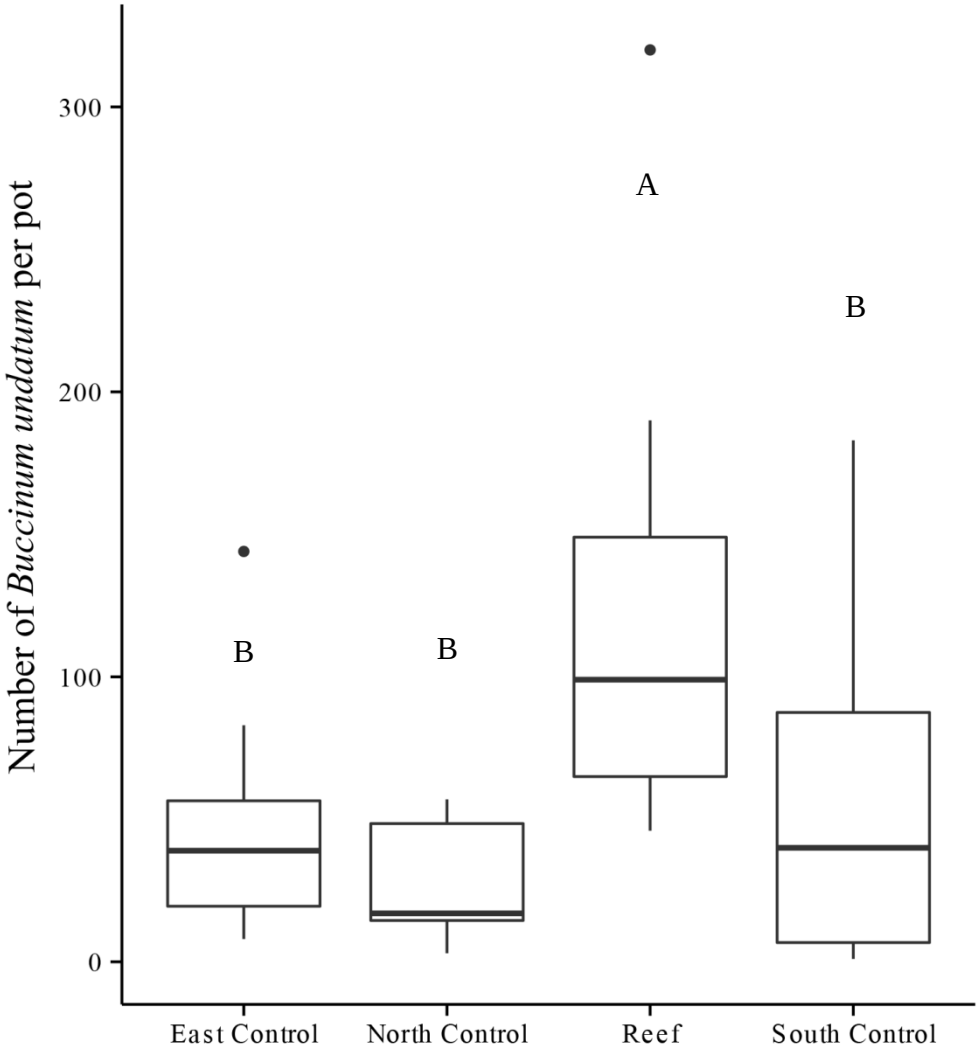

Figure 15. Whelk counts at 61 sites over four areas off the Pen Llŷn, North Wales. East Control (n=15), North Control (n=15), Reef (n=17), South Control (n=14). The upper and lower edges of the boxes show the first and third quartiles and outliers are plotted as points. Areas that share a letter are not significantly different at $p<0.05$, see appendix B3 for pairwise comparisons.

There was no relationship between *B. undatum* counts and depth ($r^2 = -0.02$, p=0.99), as shown in Figure 16. A PERMAOVA test on the size distribution of *B. undatum* at the reef and three control areas showed that depth was not a significant factor in the model (pseudo-F=1.1, p=0.37). However, area was a significant factor (pseudo-F = 10.90,

p=0.003), with the size of whelks at the reef sites being significantly different to the East Control Area (p=0.013), and the North Control Area (p=0.038). *B. undatum* at the South Control Area were smaller than those at the reef on average but the size distribution was not significantly different (p=0.21). This is also displayed in the MDS plot (Figure 18) with an overlap of the size distribution of whelks at the South and Reef sites. Overall, the analysis of *B. undatum* counts and size shows that that depth is not an important factor, but the area of seabed that the samples were collected from influences the number and size of the whelks.

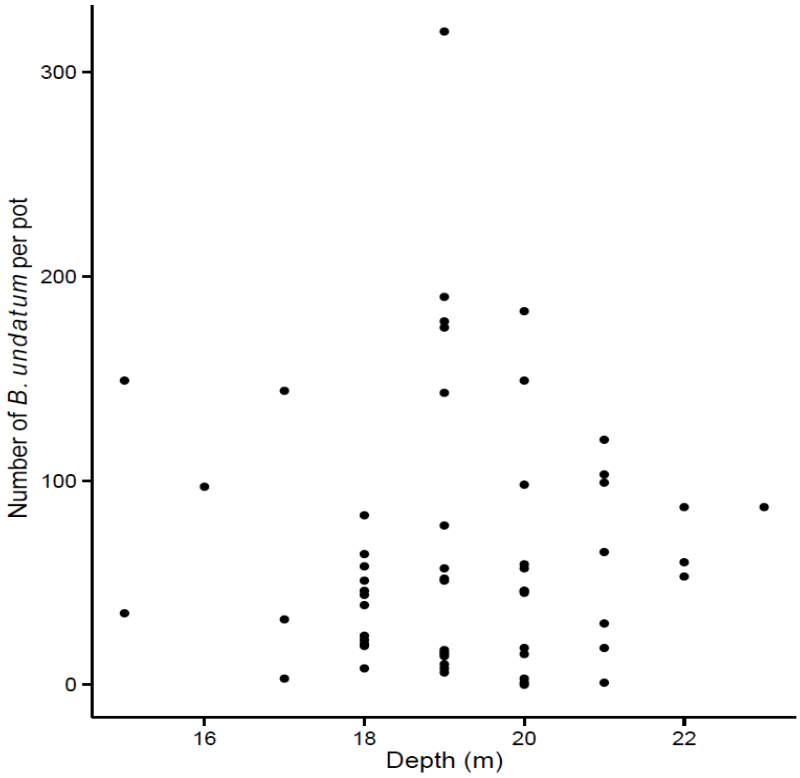

Figure 16. The relationship between *B. undatum* counts and the depth at which they were caught at 61 sites off the Pen Llyn in Wales, UK using baited pots.

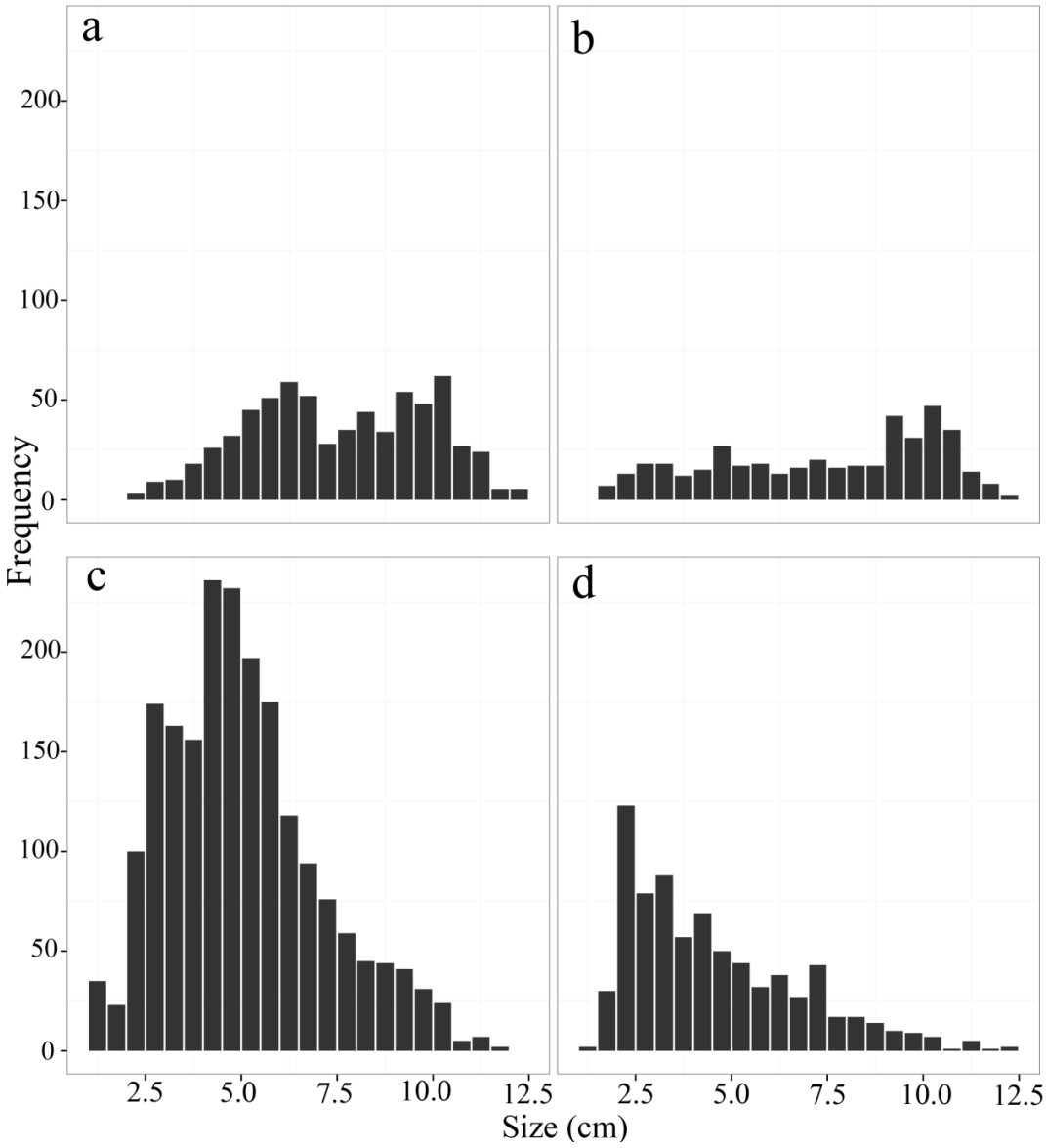

Figure 17. Size frequency distribution of whelks (*Buccinum undatum*) in the four experimental areas off Pen Llŷn, North Wales. Bars represent total counts for each size class at each area, a = East Control Area, b = North Control Area, c = Reef, d = South Control Area.

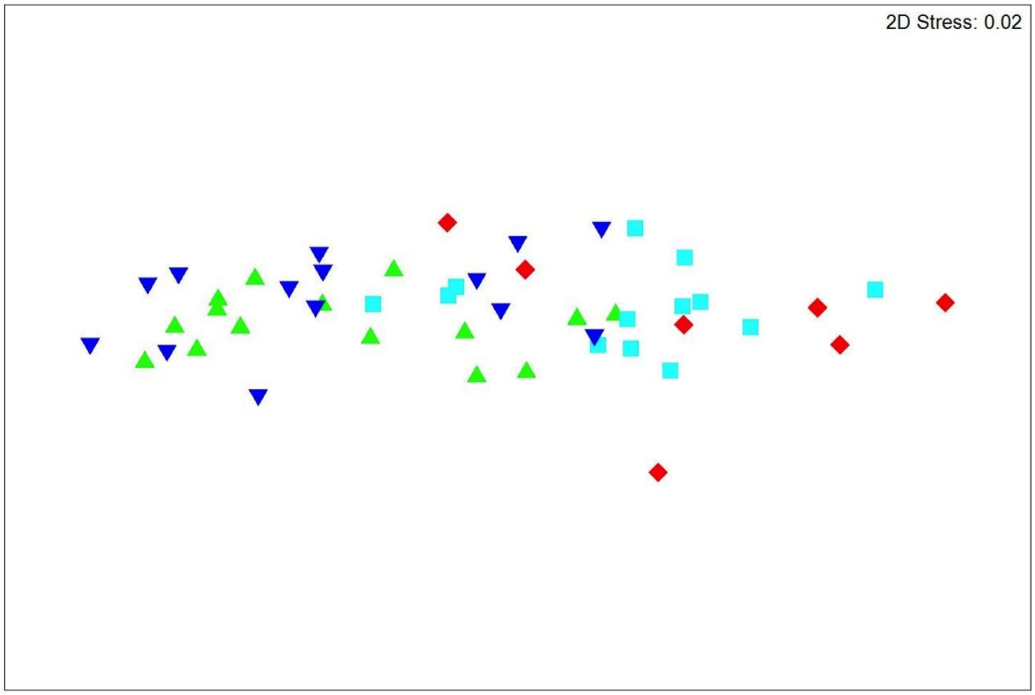

Figure 18. An MDS plot of cumulated *B. undatum* size distribution using a Manhattan Distance resemblance matrix. East Control Area = green triangles, North Control Area = upside down blue triangles, Reef Area = blue squares and red diamonds = South Control Area.

Growth Rates

Out of 377 opercula collected, 234 were possible to age with clear striae and no erosion of the opercula. *B. undatum* caught on the reef had a higher asymtopic maximum length ($L\infty$) than the North, East and South control areas, with the lowest $L\infty$ at the South Control Area. The average age of *B. undatum* caught at the East Control Area was 8.59 years, which slightly older than those at the North Control Area (7.35 years), the Reef (6.14 years) and the South Control Area (6.02 years). An ANOVA showed that the difference in age between areas was not significantly different at the 0.05 significance level ($F=2.57$, $p=0.059$). The likelihood ratio test showed a difference in $L\infty$ between *B. undatum* caught on at the four Areas ($F=2.23$, $p=0.049$). However, the estimates of $L\infty$ are much higher than those caught (maximum length caught = 12.5cm) suggesting that the VBG growth models do not fit the data well. Differences in growth rates between areas were not significantly different ($F=2.10$, $p=0.063$) and were therefore not investigated further.

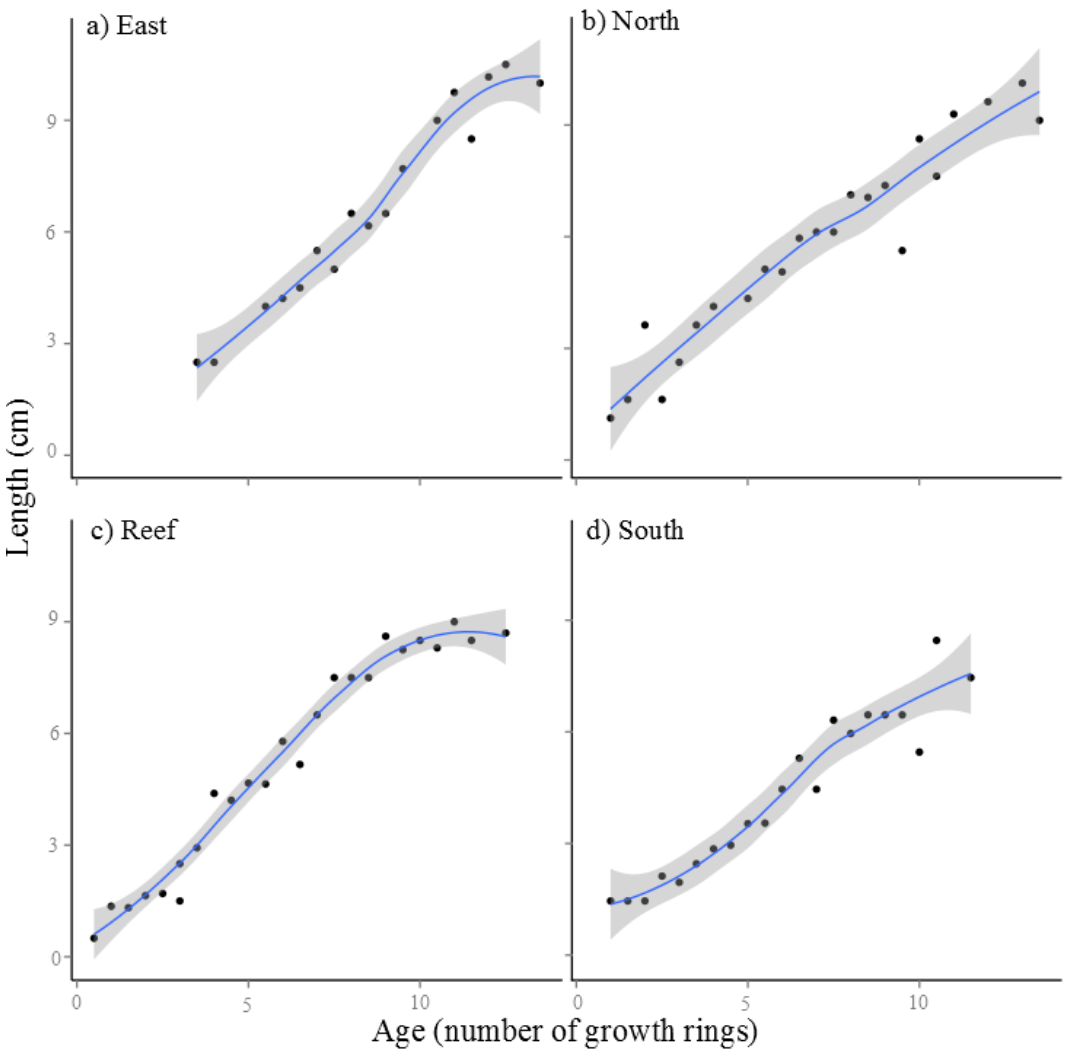

Figure 19. Growth curves for *B. undatum* caught on a) the East Control Area; b) the North Control Area; c) the reef; and c) the South Control Area using opercula growth rings where one ring = one year. Shaded area shows 95% confidence intervals.

Table 3. Von Bertalanffy maximum lengths (L∞), growth coefficients (K) and t0=theoretical age at length 0 for *B. undatum* caught in the 4 experimental areas.

	L∞ (cm)	**K**	**t0**
East Control Area	23.92	0.041	0.66
North Control Area	23.65	0.040	0.57
Reef	26.22	0.046	-0.22
South Control Area	22.03	0.037	-0.75

Tagged whelks

Cable ties were used to tag 357 whelks, which were released at three locations. Only 21 whelks were recaptured and the majority (20 whelks) were recaptured within 100m from their release location soon after they were released. However, one of the whelks released on the reef, was recaptured a year later 2567m from the release site at a location off the reef.

Table 4. Number of tagged, released and recaptured whelks and maximum distance travelled from the release location.

	Number	**Number Recaptured**			**Maximum**
Tag	**Released**	**3 days after release**	**1 month after release**	**1 year after release**	**distance travelled (m)**
Black	171	1	0	1	2567
White	52	1	0	0	0
Coloured	134	8	10	0	85

Discussion

The data collected on the Pen Llŷn *M. modiolus* reef suggest that this reef is an essential habitat for *B. undatum.* High catch rates of small *B. undatum* on the reef indicates that the complex structure of the reef is acting as a nursery ground, with young *B. undatum* utilizing the protection provided by crevices created by *M. modiolus* shells. Similarly, structurally complex habitats are often used by juvenile fish and shellfish to increase growth and survival rates (Heck Jr et al. 2003). The seabed type at the North and East Area was largely coarse sand (Robinson et al. 2011), which would provide little protection for juvenile whelks in comparison to the reef habitat.

It has been well documented that fish size is often related to depth or distance offshore (Gibson et al. 2002, Macpherson and Duarte 1991), although seawater temperature and habitat type may be confounding factors (Walsh 1992). In this study, there was no relationship between *B. undatum* size and depth, suggesting that habitat type is more important for ontogenetic habitat associations. However, the depth range was limited in this study and therefore, a more extensive study of different habitats at different depths would increase our understanding of the habitats that are used by *B. undatum.*

The whelks at the South Control area were smaller than those on the reef on average. Analysis of the video footage in this area found that the habitat here is gravel and cobbles with some macroalgae, which could provide a similar complexity to that on the reef and therefore protection for the smaller *B. undatum.* However, there were more *B. undatum* on the reef site so there were more undersized *B. undatum* (<4.5cm) on the reef in total, even though the average size was slightly larger on the reef. On two occasions, the fishermen were seen discarding undersized whelks that had been collected throughout the day on the return journey to Porth Dinllean, effectively relocating the undersized whelks, and, over time potentially influencing the size distribution at the South Control Area.

The high variation in catch rates found throughout this experiment is likely to be due to habitat heterogeneity. Drop down video footage on the reef shows abrupt changes from dense reef with erect epifauna to dead shell and sparse patches over 5-10 meters.

As well as being structurally complex, an abundance of prey items on the reef may provide an important source of energy for the whelks during a rapid growth stage early in life (Nasution and Roberts 2004). *M. modiolus* reefs have a wide range of organisms associated with them (Rees et al. 2008, Sanderson et al. 2008), including bivalves and crustaceans, which are all known to be utilised by *B. undatum* as a food source (Himmelman and Hamel 1993). This would prioritize biodiverse biogenic habitats over structurally complex habitats with low diversity in the identification of *B. undatum* EFH.

The morphological differences of *B. undatum* caught at different areas in North Wales (differences in size distributions and shell structure) is consistent with the theory that less mobile, direct developing species are more locally adapted than planktonic developers (Yamada 1989). In the Irish Sea, *B. undatum* reach sexual maturity at 6-7cm shell length (Kideys 1994), and this study has shown that there is a high proportion of small (<5cm) *B. undatum* on the reef and large (>6cm) *B. undatum* at the North and East Control areas. If the large *B. undatum* are moving off the reef, this could have implications for breeding and dispersal of the population, with fewer mature whelks on the reef for sustaining the population here. However, the fishermen reported seeing whelk egg masses on their pots at all the reef sites, suggesting that this is not an issue.

Weetman et al. (2006) carried out genetic analysis of *B. undatum* across the European continental shelf over large geographical scales (i.e. between the UK and Iceland), and small spatial areas (e.g. within the Clyde Sea, Solway Firth and Carmarthen Bay). This showed differentiation but only across large scales and *B. undatum* were able to migrate within local areas on a scale of ~10km. This suggests that the *B. undatum* populations on the Pen Llŷn *M. modiolus* reef and the three control areas (mostly only 3-4 km apart) are not distinct populations, but are in fact the same population. This is reinforced by the fact that one whelk in this study travelled 2.5km in one year and although it would be unwise to infer migration patterns of a population from one individual, this result shows that it is possible for *B. undatum* to travel this distance. Furthermore, the whelk moved from the reef to an 'off-reef' area, which, in combination with evidence that the reef supports high numbers of small individuals, could imply that the reef is a nursery ground for whelks and may have a 'spill-over' effect by supplying surrounding areas with whelks that originate from the reef, which has been shown to be the case for coral reefs in MPAs (Tupper 2007, Kaunda-Arara and Rose 2004, Francini-Filho and Moura 2008). However, a much more detailed tagging experiment would be required to validate this theory for *M. modiolus* reefs.

Analysis of operculum growth rings showed no significant difference in growth rate between the *B. undatum* caught at the four experimental areas. Higher growth rates of shellfish (*Mercenaria mercenaria*) have been found on biogenic habitats, which was attributed to food availability (Arnold et al. 1991). However, this was on a scale of 120km whereas in the present study, sites were much closer together therefore, whelks may be moving between areas and so food availability would not manifest as a difference in growth rates. However, the growth rate analysis study was limited by the low number of opercula successfully analysed and it is therefore difficult to draw conclusions from this aspect of the investigation.

The technique used to count operculum rings does involve some error especially on older individuals because larger opercula occasionally showed areas of erosion due to the operculum being in close contact with the seabed, making it difficult to count the rings. This can have implications for the calculation of maximum length and growth rate. Many opercula samples were rejected due to unclear striae and in future studies, more operculum samples would need to be collected and analysed to investigate differences in growth rate at this scale to account for those opercula that are disregarded

due to unclear striae (Kideys 1997). Furthermore, a combination of operculum growth ring counts and analysis of statoliths to examine subtle differences in growth rates should be used. This method has been shown to be effective in dog whelks (*Nassarius reticulatus*) (Chatzinikolaou and Richardson 2007).

M. modiolus reefs are sensitive to physical impact from mobile fishing gear (Cook et al. 2013) and extensive reef areas have seen a decline in *M. modiolus* habitat (Strain et al. 2012). The small scale whelk fishery on the Pen Llŷn is an important part of the local economy employing 12 fishers from one village, therefore, without the appropriate protection of this habitat the whelk fishery could see a decline in catch rate if the reef experiences a decrease in size or condition. Sustained pot fishing for the past twenty five years on the north coast of the Pen Llŷn and the high catch rates shown here, combined with low recapture rates suggests a considerable population of *B. undatum* in this area.

Chapter 4. *In situ* measurements of sedimentation and biodeposition on a *Modiolus modiolus* reef

Abstract

Horse mussels (*Modiolus modiolus*) can occur in dense aggregations to form biogenic reefs. *M. modiolus* reefs build up over time to form raised structures on the seabed and this three dimensional structure is largely made up of biodeposits, shell material any byssus threads. A method was developed to measure sediment deposition *in situ*, on a *Modiolus modiolus* reef. Results show that *M. modiolus* reefs enhance sedimentation and contribute to the downward flux of material to the seabed. Using this technique, it is possible to show the relative contribution of active (bivalve filtration) and passive processes (modification of the boundary layer hydrodynamic structure) occurring and to determine the overall accumulation of sediment under natural conditions. A high proportion of organic rich sediment accumulated in the live *M. modiolus* treatment due to deposition of faeces and pseudofaeces, which provides an importance source of energy for benthic infaunal species living on the reefs as well as enhancing bentho-pelagic coupling. The experimental procedure described here is the first of its kind to show the scale at which *M. modiolus* reefs are able to perform these important ecological functions and provide ecosystem services to society.

Introduction

Sediment deposition in marine systems is primarily controlled by physical processes such as currents and waves, and chemical processes such as the cohesive forces acting between fine clay particles (Montserrat et al. 2009). The presence of biogenic structures such as mussel beds, increases the surface roughness of the seabed, which modifies the flow, disrupts the benthic boundary layer (Figure 20, process 2) and enhances sediment deposition (van Leeuwen et al. 2010). This is modified further by the active filtration process carried out by mussels (van Duren et al. 2006). Biogenic structures can also influence sediment grain size and quality by biological processes such as bioturbation (Willows et al. 1998) and biodeposition (Mayer et al. 1985).

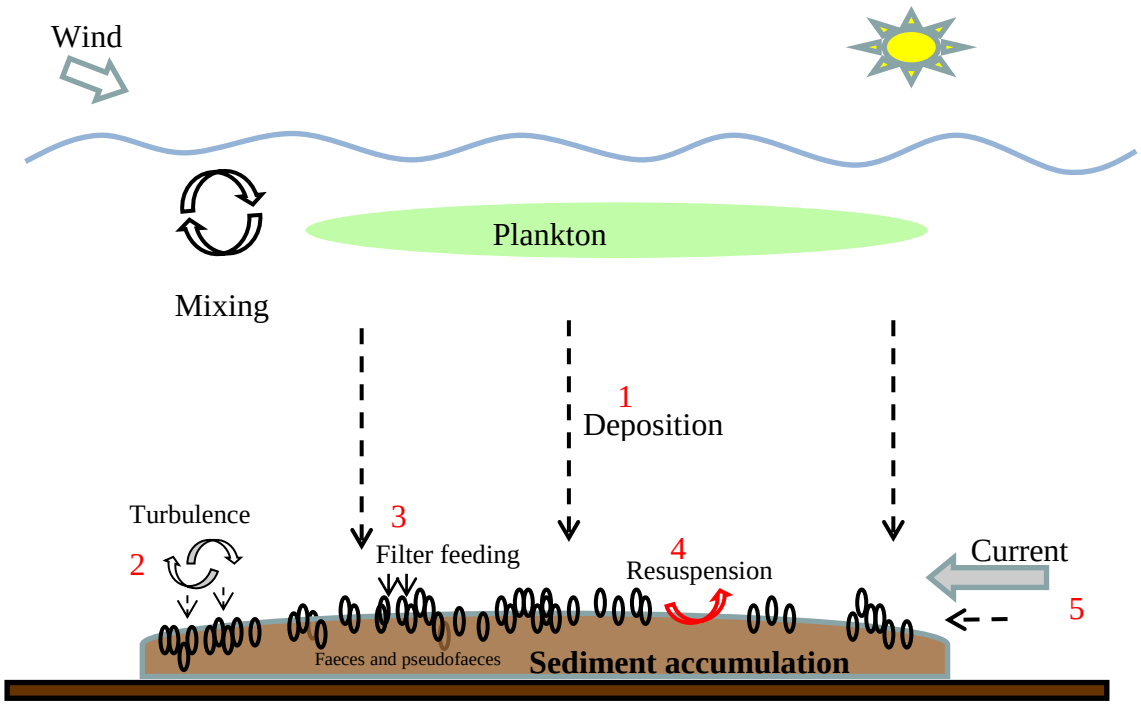

Figure 20. Six sediment processes occurring on a biogenic structure based on 1, Lampitt (1985); 2, van Leeuwen et al. (2010); 3, van Duren et al. (2006); 4, Doering (1989); 5, van Duren et al. (2006).

Many of the processes illustrated in Figure 20 vary daily and seasonally, for example due to the response of phytoplankton to seasonal changes in nutrient and light availability and are modulated by mixing i.e. storms (Baileywatts 1978). Resuspension can become an important process in tidal areas such as sea lochs (Overnell and Young 1995), and sediment deposition can also vary on a spring-neap tidal cycle.

Bentho-pelagic Coupling

Filter feeders act as a top-down control on phytoplankton production and eutrophication (Soto and Mena 1999) and are therefore ecologically important. Benthic filter feeders such as mussels, are exposed to a range of suspended particles including plankton, detritus and mineral grains of various sizes (Ward and Shumway 2004). Variations in the seston concentration, or Total Particulate Matter (TPM) that is available to filter feeders are in part caused by the local tidal regime, with greater resuspension occurring during spring tides (Hawkins et al. 1996).

A great deal of research has been carried out into feeding and biodeposition rates of bivalves such as *Mytilus edulis*, and other commercially important species however,

information on non-commercial shellfish species such as *M. modiolus* is often lacking. Biogenic reef forming filter feeders are able to mediate the quality of the material that reaches the seabed (Navarro and Thompson 1997) and therefore play an important role in coupling pelagic and benthic systems in the flow of organic material. This material is also recycled back into the pelagic ecosystem through resuspension and the reef fauna assimilate the energy into their tissues, making it available for higher trophic levels. By filtering large volumes of water and removing suspended particulate matter, shellfish act as a natural cleansing tool (Zhou et al. 2006) adding to the importance of these species for bentho-pelagic coupling. *M. modiolus* reefs also provide a habitat for mobile species (chapter 2 and 3), which may influence bentho-pelagic coupling further. Bray et al. (1981) show that mobile species are able to redistribute energy from the pelagic system to the benthos if they spend the day feeding on zooplankton and use a rocky reef as a nocturnal habitat where faeces are deposited.

In bivalves, the products of the water filtration process are partly channelled into metabolism and growth of the animal, but some is packaged into faeces and pseudofaeces. On a *M. modiolus* reef this can be observed by the raised structure of the reef which consists of a matrix of dead shell, biodeposits and animal remains which can form an undulating wave formation on the seabed (Lindenbaum et al. 2008). Rees et al. (2008) report distinct 'sub habitats' within a reef, with abundant crevice fauna on the ridges of the reef and accummulation of dead shell in the troughs. Analysis of the sediment on a *M. modiolus* reef showes a bimodal particle size distribution with very fine sand and silt/clay within the living reef ridges (Nic Aonghua et al. 2001), which is likely to be a result of biodeposition. Furthermore, the carbonate content of the reef was up to 60% in some areas, as a consequence of the accumulation of dead shell material.

Bivalve Feeding and Deposition Measurements

Accurate measurements of bivalve feeding are difficult to achieve in the laboratory due to the unrealistic environmental setting. However, experiments have been carried out in 'semi-natural' conditions with seawater pumped through chambers on piers, pontoons or research vessels (Hawkins et al. 1996, Yaqin et al. 2009, Galimany et al. 2011, MacDonald and Ward 2009). However, inshore surface seawater conditions are likely to be quite different to the deeper, more exposed locations where *M. modiolus* reefs occur

Direct measurements of biodeposition rates occurring *in situ* have the benefit of being exposed to natural conditions yet have rarely been attempted due to the nature of these subtidal habitats being in difficult working environments. Yahel et al. (2005) were able to calculate feeding rates by taking water samples from the inhalant and exhalent siphons of bivalves, ascidians and sponges *in situ* using SCUBA divers. Zhou et al. (2006) measured scallop biodeposition rates *in situ* using PVC cylindrical traps suspended under a longline in order to recreate the conditions the animals would be exposed to when cultured. Scallops were placed between two nets at the top of the tube and biodeposits collected at the bottom of the cylinder. However, Storlazzi et al (2011) warn against the use of cylindrical sediment traps to achieve absolute measures of deposition due to the modification of hydrodynamics around the trap, which can influence the total amount of sediment obtained.

Bivalves can also influence the physical properties of the surrounding water on a small scale through their pumping mechanism, which can create jets of water into the benthic boundary layer. Lassen et al. (2006) for example, found that the water expelled from the exhalent siphon of *M. edulis* can enhance down-mixing of phytoplankton, and this is more effective at lower flow speeds. According to Asmus and Asmus (1991), filter feeders can also induce local primary production due to resuspension of the material that they produce.

Results from experiments using natural seston rarely agree with those where bivalves are fed on artificial food in controlled conditions (Wong and Cheung 1999, Iglesias et al. 1996). Hawkins et al. (1996) found that, when supplied with natural seston only, the efficiency by which *M. edulis* select organic material increases with filtration rate, particularly when the organic content of the seston is high. In addition, *M. edulis* preferentially reject inorganic matter with pseudofaeces. Velasco and Navarro (2005) suggest that natural seston contains a greater diversity of particles, and when comparing laboratory experiments (using artificial feed) to *in situ* experiments (e.g. using flow-through chambers), found that clearance rate and selection efficiency were similar under both experimental conditions. However, filtration rate, ingestion rate, absorption rate and absorption efficiency were significantly higher in laboratory experiments.

An alternative to measuring direct feeding rates is to measure the net accumulation of material over time on a shellfish reef. Ten Brinke et al. (1995) measured sedimentation

rates of 5 – 20cm per year using radio isotopes in sediment cores on a *M. edulis* bed. Further measurements were made using experimental plots with marked pipes; divers returned to the plots over time and measured the increase in sediment from the mark. The results showed increased sedimentation in plots with adult mussels but no increase in plots with juvenile mussels. Collection of material deposited on steel plates in these plots showed that pellets made up approximately 20% of the sediment. For very shallow or intertidal beds, presumably the reefs reach a maximum height before wind and waves resuspend the sediment and limit the total bed height. This is probably not the case for *M. modiolus* reefs which are subtidal and tend to occur in depths >20 meters.

The Reef Effect

It has been suggested that when mussels occur in high densities to form beds or reefs, the mussel assemblage may significantly influence the surrounding water column and increase the overall filtration rate of the bed or reef. For example, Widdows et al. (2009) measured current velocities and near-bed shear stress over a mussel bed in the Menai Strait, and compared this to an area of bare mud. This information was combined with flume tank experiments to show that mussel assemblages induce resuspension of sediment, which enhances feeding activity and causes large scale clearance of particles from the water column. In addition to the active and passive processes occurring on a *M. modiolus* reef, it is expected that there would be an influence of the mussel assemblage itself (Schwindt et al. 2004), which may further enhance deposition. This process will be referred to as the 'reef effect' for the purposes of this study.

The aim of this study is to measure the rate of sedimentation *in situ*, on a *Modiolus modiolus* reef and to understand the relative scale of the passive and active sedimentation processes occurring on the reef (Figure 20, processes 2 and 3). Gaining an understanding of the scale of the functional processes occurring on the reef will help to estimate the value of biogenic reefs such as those created by *M. modiolus.* Further to this, sedimentation rates will be compared at sites on and off the reef to investigate the 'reef effect' as mentioned above. This experiment will test the hypotheses that: 1) live *M. modiolus* enhance sedimentation by active biodeposition; 2) the physical structure created by *M. modiolus* increases sediment deposition by passive processes; and 3) *Modiolus modiolus* reefs increase sedimentation.

Methods

Sampling took place at two sites in Loch Linnhe, Scotland (Figure 21), one on a *M. modiolus* reef, 56° 33’ 1.8’’ N, 005° 25’ 26.4’’ W, and an ‘off-reef’ control site to the north-east of the reef at 56° 33’ 56.59’’ N, 5° 24’ 29.95’’ W. Both sites were at 22m below chart datum, on a gently sloping seabed. Twenty-four experimental units were deployed using SCUBA divers. Each experimental unit consisted of a 6 litre container with a 4cm thick layer of concrete inserted into the bottom to weigh the unit down, and this was covered in a layer of scouring pad (Figure 22 B). The scouring pad material was used to ensure that the sediment and biodeposits remained in the box and were not resuspended, following Babcock and Smith (2000). An o-ring on the lid created a seal so that no sediment would be lost during retrieval. Each experimental unit was pinned to the seabed using 1.25m steel rods.

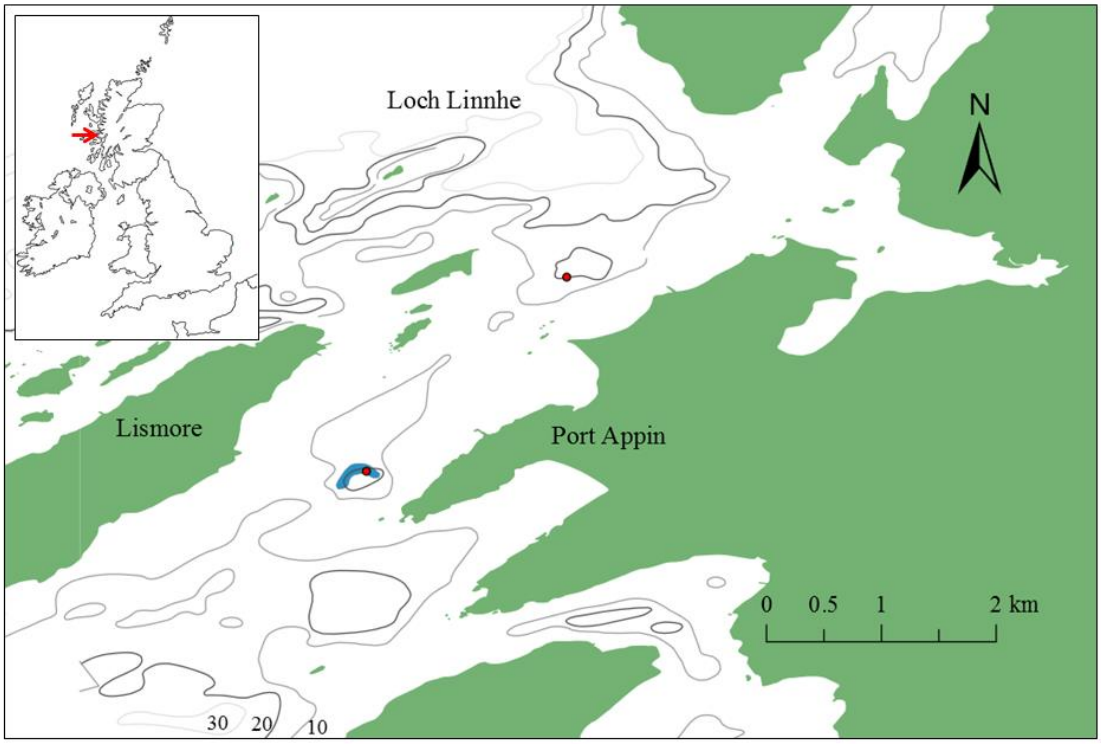

Figure 21. Site location with UK map insert, inset shows the location of Loch Linnhe, experimental sites are represented by red circles. *M. modiolus* bed to the south-west and control site to the north-east. Blue polygon shows the estimated *M. modiolus* reef outline from (Moore et al. 2012).

Experimental Design

At each site, four of the experimental units contained three live *M. modiolus* (10.5-12.5cm in length), four contained three 'dead' *M. modiolus* (shells held together with concrete), and four contained no *M. modiolus*. Mussel density at the reef site had been recorded the year before (Moore et al 2012), and therefore, the number of animals in the Live and Dead treatments were chosen to represent this natural density (approximately 40 mussels m^{-2}). Live *M. modiolus* had been collected on the 19/06/2012 and kept in a mesh bag attached to a nearby pontoon to reduce disturbance to the mussels during transportation etc. To control for the 'box effect', four scouring pads were deployed at each site on plastic tiles (Figure 22 A).

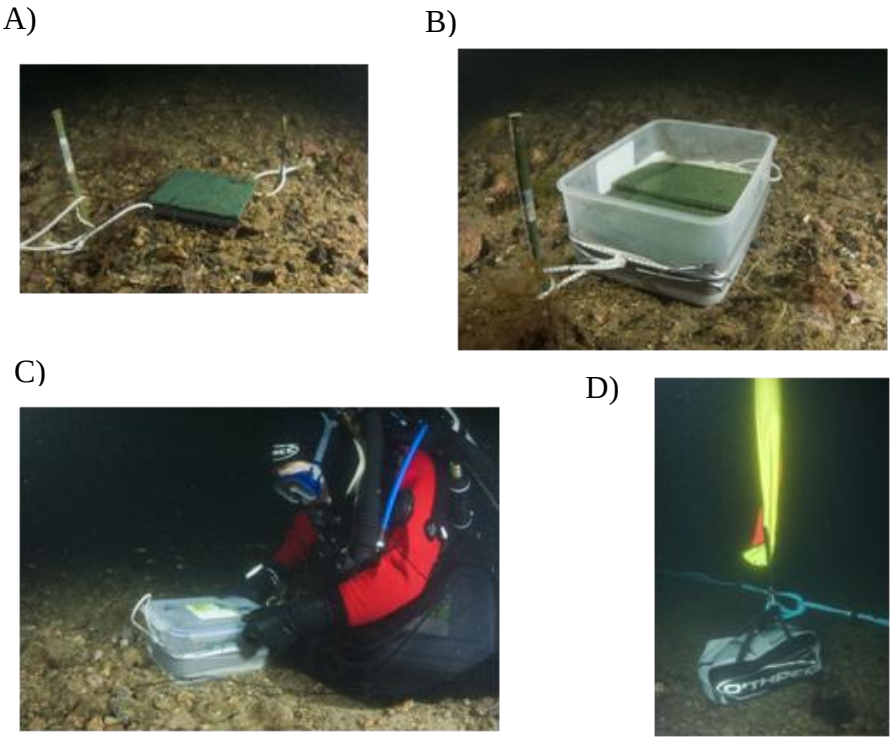

Figure 22. Images showing deployment and retrieval of the experimental units, A) shows the scouring pad controls, B) control boxes, C) and D) retrieval of the experimental units. Images: Rob Cook.

The experimental units were distributed at random around a central marker on the seabed in two concentric rings to ensure even exposure of all boxes from currents at all tidal states (Figure 23). Each treatment was 2.5m from the next in the circle. The boxes were deployed with lids on and the tiles were transported to the seabed in plastic zip-lock bags. Once the divers had distributed the treatments, the lids and bags were removed starting with the upstream boxes and tiles to minimise the risk of disturbed sediment entering the experimental units.

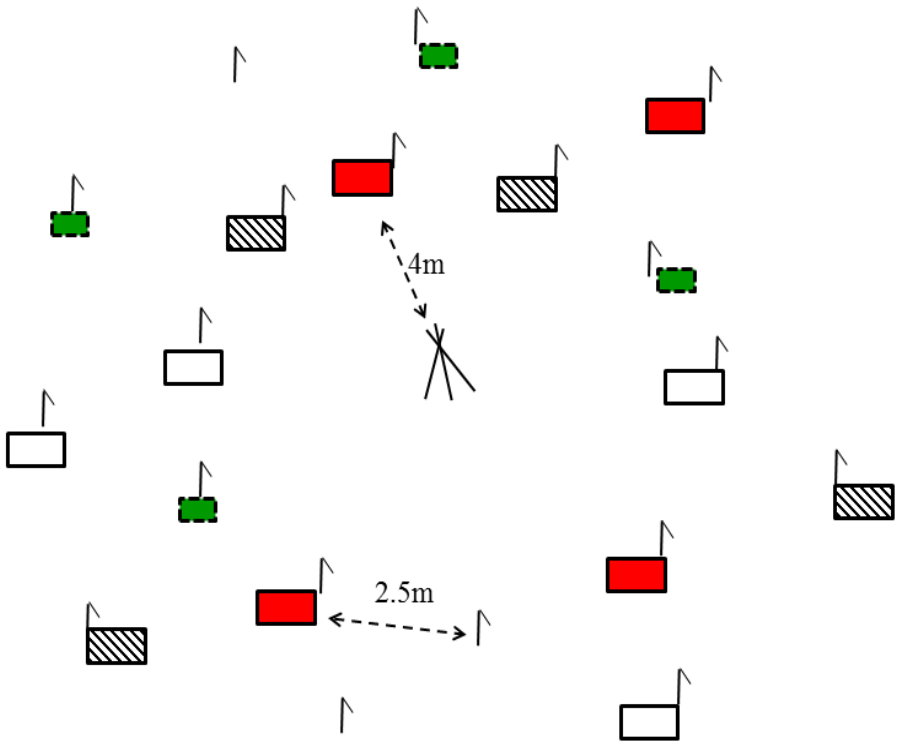

Figure 23. Diagram of the site layout at one site. Green squares = control scouring pads on tiles, white squares = empty boxes, red squares = boxes with dead mussels and checked boxes = boxes with live mussels.

The experimental units were left on the seabed on the 10/07/2012 for 7 days. During recovery, lids were placed on all boxes and tiles were placed in bags starting downstream and working upstream to avoid any resuspended sediment created by the divers entering the boxes. All boxes were lifted to the surface in large bags and the tiles were carefully placed into zip-lock bags and carried to the surface by the divers. Six tiles were left at each site so that three could be retrieved one week later and the final three to be retrieved one month later to measure the saturation point of the scouring pads, and to ensure that the scouring pads in the boxes were not becoming saturated during the seven day experiment.

The horse mussels and scouring pads in the boxes were rinsed off, and the water was filtered on pre-ashed Whatman GF/C filters (1.2μm pore size) following Navarro and Thompson (1997), then rinsed through with distilled water to remove salt. Water from the zip-lock bags was stored in sample buckets and the scouring pads rinsed until the water ran clean. The water from the scouring pad samples was also filtered. The filters were dried at 100°C until they reached a constant weight, then ashed at 450°C for two hours following Bayne et al. (1993). The organic fraction of each sample was calculated by dividing the weight Loss On Ignition (LOI) by the weight of the Total Particulate Matter (TPM). Before measuring LOI, a 250ml sub sample was taken from each sample and frozen for particle size analysis using a Coulter LS230 laser diffraction particle size analyser (Beckman-Coulter, USA).

Data Analysis

TPM was converted to gm^{-2} by dividing the weight of the sediment by the area over which it was collected, in order to scale the results up to an ecosystem scale. The TPM data were square root transformed and tested for normality (Anderson Darling test, $p=0.32$) and equal variances (Bartlett test, $p=0.88$). The TPM collected from the experimental units at the control site was compared to those at the reef site using a t-test. In order to test for differences between treatments, an ANOVA was used with Tukey post-hoc multiple comparison tests. The scouring pad saturation data was analysed using a linear model and all univariate analyses were carried out in R version 2.9.1 (R Development Core Team 2011).

To compare the results to others in the literature (Navarro and Thompson 1997), data were treated differently; the weight of sediment deposited was converted to mg day^{-1}

mussel $^{-1}$. Then, the average sediment deposited by control (dead) mussels was subtracted from that deposited by live mussels to account for any background deposition and therefore estimate the active biodeposition rate.

The total weight of organic material determined by loss on ignition (LOI) for each sample was log transformed and tested for normality (Anderson Darling test, p=0.22) and homogeneity (Bartlett test, p=0.08). Following this, the data were analysed in the same way as TPM. The total organic content was then calculated as a proportion of TPM to give the fraction of organic content of the seston (f). This converted data (f) did not meet the criteria for a parametric test and were therefore compared using a Kruskal-Wallis test.

The particle size fractions were standardised as a proportion of the total weight of the sample and cumulated. Multidimensional scaling ordination was performed on the cumulated particle size distribution data (Clarke 2006) based on Manhattan distance (see chapter 1, data analysis). An analysis of similarities (ANOSIM) was used to compare the particle size between the two sites and the four treatments.

Results

Scouring Pad Saturation

The scouring pads continued taking on sediment throughout the 51 day saturation experiment and fit to the linear model $y = 9.4x – 9.43$. This data give reason to believe that the experimental chambers used in the *in situ* sediment accumulation experiment did not become saturated during a 7 day experiment. Variation between replicates was small after 7 and 21 days (SE= 4.04 and 3.89 respectively) but increased at 57 days (SE=23.94).

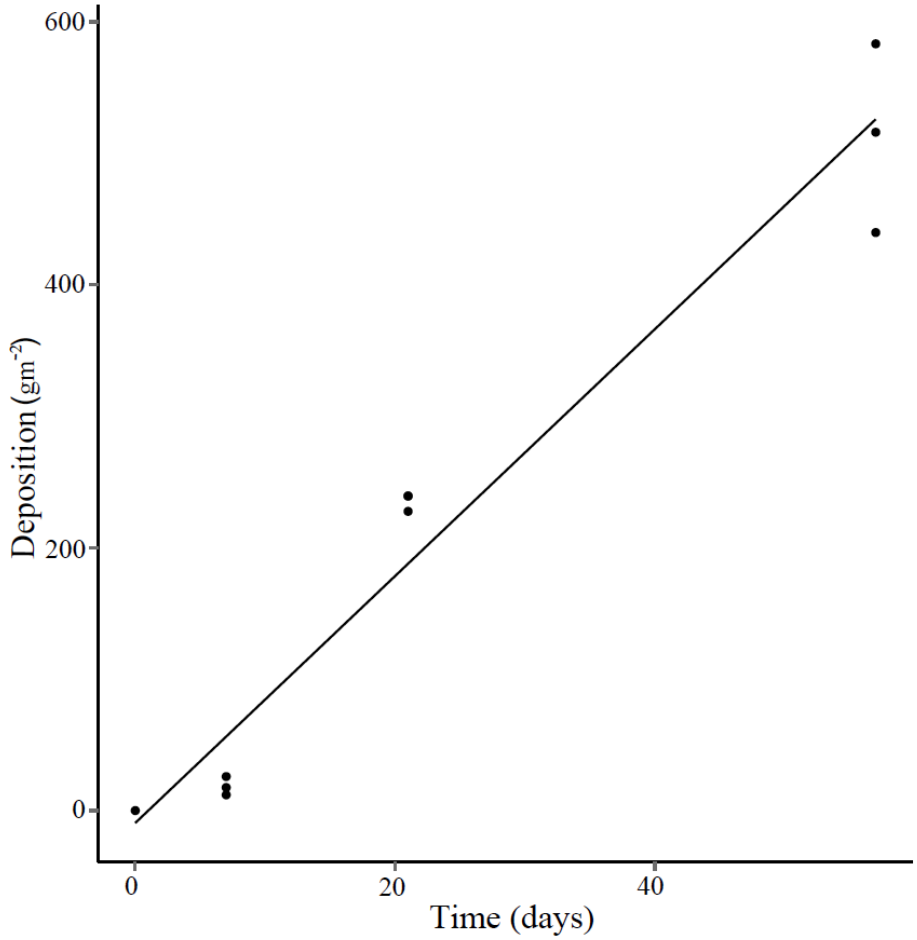

Figure 24. Sedimentation on scouring pads at Port Appin, spring 2012 (gm^{-2}).

Total Particulate Matter

There was no difference in TPM in any of the treatments at the off reef site (no *M. modiolus* present) compared to those at the *M. modiolus* reef site (t test, p=0.82). However, the average TPM (± 1 SE) in the live treatment was 64.42 ± 4.91 g m^{-2}, which was significantly greater than the Dead treatment (ANOVA, p=0.04) and the control boxes (ANOVA, p=<0.001). The dead mussel treatment was also significantly different to the control (ANOVA, p=0.04), as shown in Figure 25. This suggests that the physical structure of the mussels does contribute to sediment deposition on mussel reefs and the active filtering process enhances deposition further. The difference between the deposition in the live and dead chambers was 19.28 gm^{-2} (approximately 30% of the total sediment deposited). There was no significant difference between the scouring pads and the control boxes (p=0.75), suggesting that there was no box effect. When calculated as biodeposition rate (faeces and pseudofaeces) for an individual

M. modiolus, values range from 0.90mg mussel^{-1} day^{-1} to 14.33mg mussel^{-1} day^{-1} with an average (±1SE) of 4.92 mg mussel^{-1} day^{-1} ±1.74.

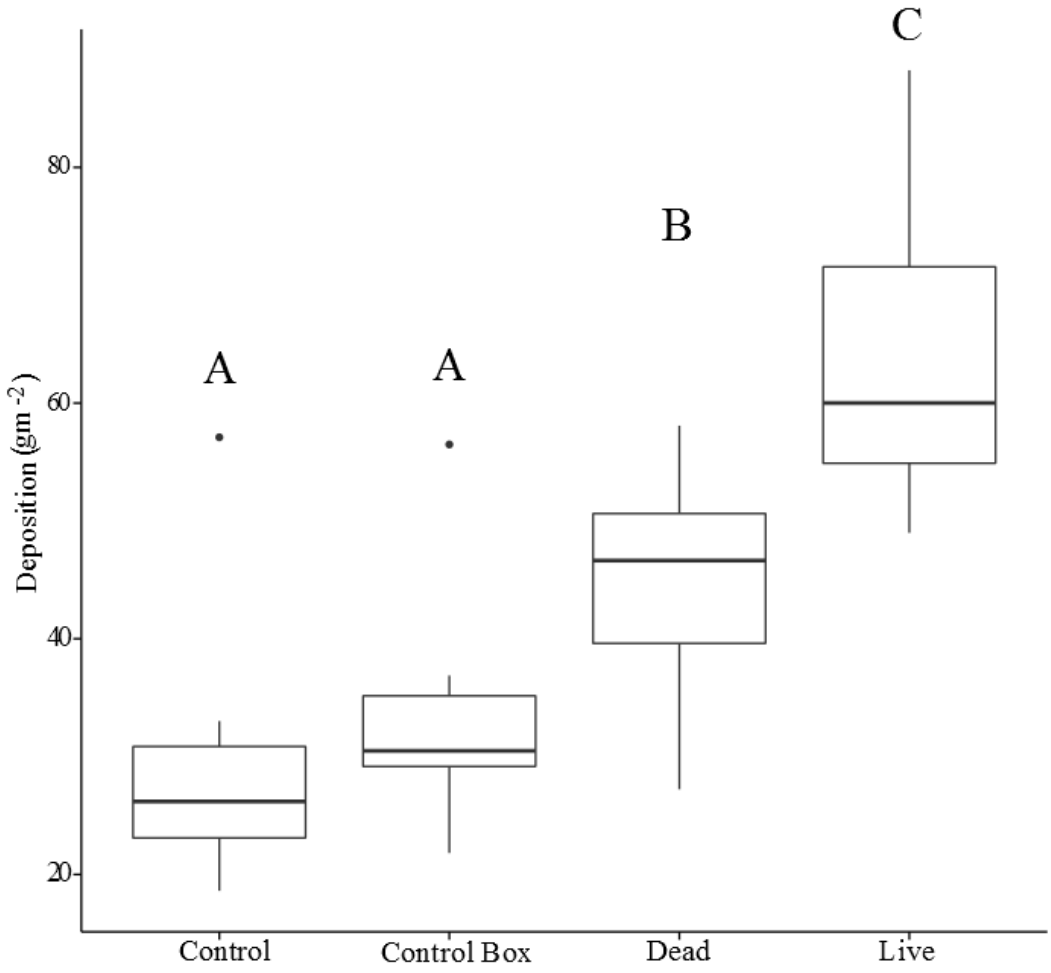

Figure 25. Total Particulate Matter (gm^{-2}) collected *in situ* in sediment traps at Port Appin Control site and *M. modiolus* (pooled data) site over 7 days. Treatments that share a capital letter are not significantly different (p>0.05). The upper and lower edges of the boxes show the first and third quartiles and outliers are plotted as points.

Organic Content

The experimental treatments were found to have a significant impact on the total organic content of the sediment collected (R^2 = 0.68, p=<0.001). Sediment from the live treatment had over three times more organic material than that of the dead (12.25gm^{-2} in the live treatment compared to 3.89gm^{-2} in the dead, p=0.02). This was also significantly greater than the control box treatment (p=<0.001) and control scouring pad treatments (p=<0.001). However, when expressed as a proportion of the TPM, there was no significant difference in organic content between treatments (X^2 =2.48, p=0.48),

although the proportion of organic material was slightly higher in the live mussel treatment compared to the control (20% and 15% respectively).

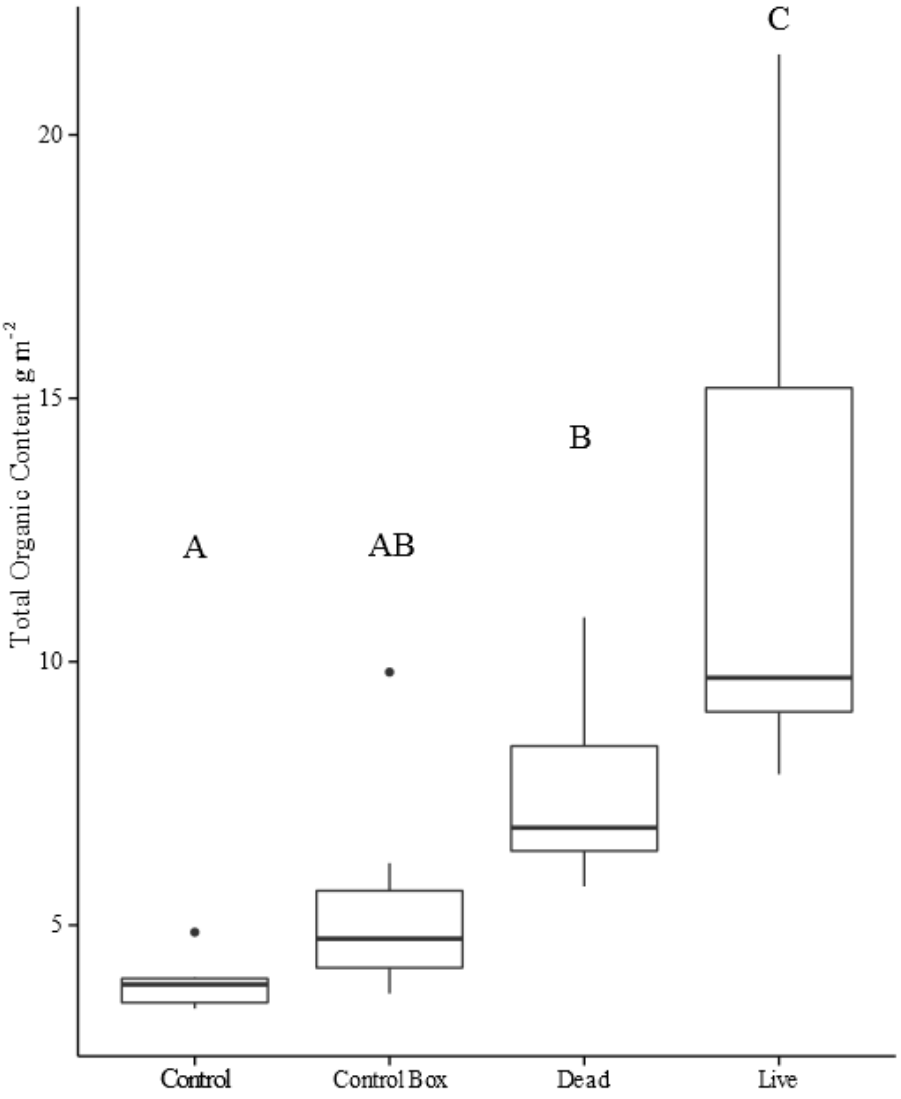

Figure 26. Total Organic Content of sediment collected *in situ* over 7 days. Treatments that share a capital letter are not significantly different (>0.05). Upper and lower edges of the boxes show the first and third quartiles and outliers are plotted as points.

There was no difference in particle size distribution between reef and off reef sites (ANOSIM, p=0.73) or treatments (ANOSIM, p=0.51). Sample B4 (a control box treatment from the off-reef site) had the lowest median particle size (17.59um) and the highest proportion of fine silt (15.4%) and clay (5.7 %), whereas sample A2 (a dead mussel treatment from the off-reef site) had the highest median particle size (23.28).

The variability in particle size distribution is relatively high (global r =-0.021), especially for the live mussel chambers (Figure 27, light blue square symbols). Appendix C2 shows the cumulated particle size distribution for each site in more detail.

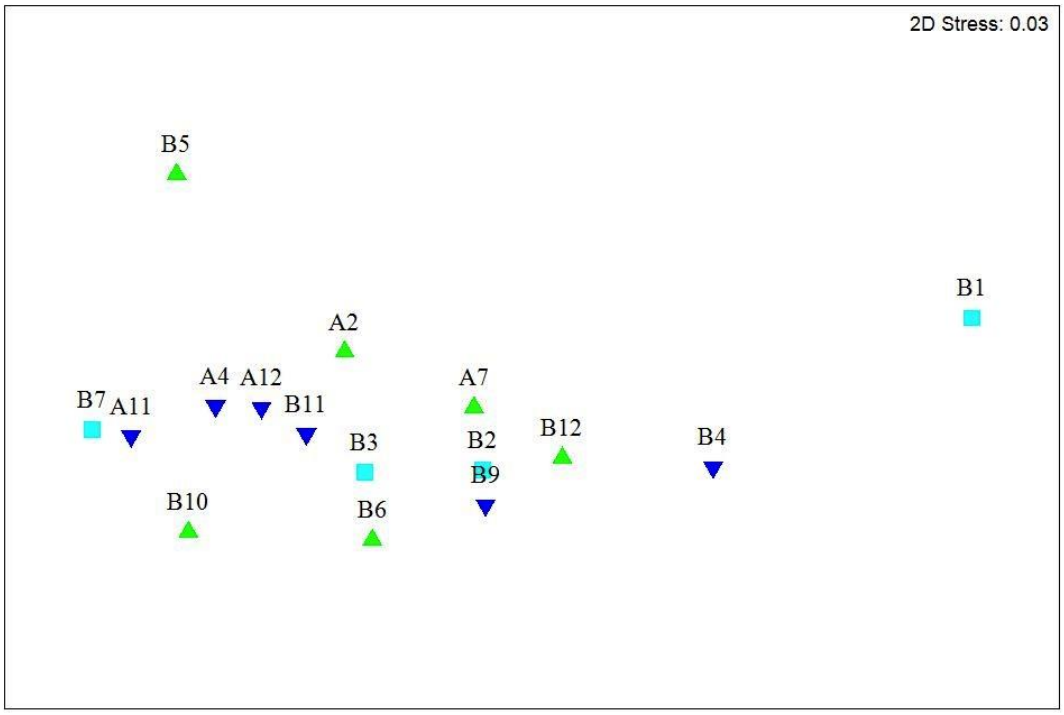

Figure 27. MDS plot showing particle size distribution of sediment from the Live (light blue squares), Dead (green triangles) and Control treatments (inverted blue triangles) based on Manhattan distance. Labels indicate samples from the reef sites (B1-7) and off reef sites (A2 -12).

At the end of the 1 week deployment, 13 crustaceans had settled in the experimental chambers (see appendix C3). Of these, 7 were in the chambers with dead *M. modiolus* and 6 were in the chambers with live *M. modiolus.* Three species of crustacean were trapped in the chambers, *Pisidia longicornis, Galathea intemidea* and *Palaemon serratus.* There were no crustaceans in the empty (control) chambers. A Kruskal-Wallis test showed that the type of chamber significantly influenced the number of crustaceans trapped in the samples (p=0.01), but site (reef or off-reef) was not a significant factor (p=0.29).

Discussion

The aim of this experiment was to design a method to measure sedimentation rates on a *M. modiolus* reef and from this, calculate the contribution of active and passive processes towards the overall accumulation of sediment on a natural *M. modiolus* reef. The experimental units that were deployed and recovered successfully provide evidence of the scale at which *M. modiolus* are able to increase sediment deposition, not only by active biodeposition, but also via passive processes. As a whole, *M. modiolus* enhance deposition two fold, from a background deposition rate of 32 gm^{-2} to 64 gm^{-2}, and of this, 41% of the enhanced deposition is due to the physical structure of the *M. modiolus* (represented by dead mussel shells). Although *M. modiolus* biodeposition rates have been measured before in an aquarium setting (Navarro and Thompson 1997), this is the first time that *M. modiolus* deposition has been quantified *in situ* on a natural biogenic reef.

The variability in organic material and particle size distribution in the chambers with live mussels is high compared to the controls. This is unsurprising as it is has been shown that the feeding behaviour of individual *M. modiolus* can vary considerably over a short period of time, for example, Navarro and Thompson (1996) recorded clearance rates of between 0 and 4.38 $l\ h^{-1}$ over a 1 hour period for one individual *M. modiolus*. *M. modiolus* were in natural conditions in the present study, however, some of the mussels may have become more stressed than others during the handling procedure and as a consequence, not resumed normal feeding activities during the experiment. Further video observations of shell gape (as a proxy for filtration) in the laboratory reveal extreme between individual variability (pers. comm. Z. Hutchison). Conversely, the control chambers do not have this natural biological component, which may provide an explanation for the lower variability observed in the control treatments.

M. modiolus are large bivalves and known to filter large volumes of water ($1 – 4\ l\ h^{-1}$; Navarro and Thompson (1996)), making them very effective pumps. The result of this pumping activity is that a large quantity of faeces and pseudofaeces are produced. However, filtration rate is dependent on a number of factors, in particular food availability. Bivalves are able to select particles to ingest based on their nutritional quality (Hawkins et al. 1996) and even the size and shape of particles (Ward and Shumway 2004). Therefore, if the mussels are exposed to a high inorganic sediment load, they produce more pseudofaeces (Hawkins et al. 1996), and at very high sediment

loads (above 1mg l^{-1}) filtration rate can be greatly reduced due to the increased energetic cost of producing pseudofaeces (Madon et al. 1998).

In the present study, there was no difference in sedimentation between the reef samples and the off-reef control site samples. The increase in sedimentation caused by live *M. modiolus* was a relatively small proportion of the total amount of sediment deposited into the experimental units (approximately 30%) suggesting that there is a large amount of background deposition. This is a similar proportion to that measured *in situ* by Ten Brinke et al. (1995), using sediment cores that were analysed under a microscope and found to contain 20% mussel pellets by volume in the top 4cm of a *Mytilus edulis* bed.

The relatively small contribution of sediment caused by biodeposition relative to background deposition makes it difficult to detect a 'reef effect' as described by Jones et al. (2011). Future experiments would need to make use of a number of different control sites that represent a range of environmental conditions, or use an area which historically contained a *M. modiolus* reef that no longer exists. Furthermore, the reef used in this study is only 2 ha (Figure 21) and does not show the same undulating reef formation as the larger, more dense reefs recorded by Hirst et al. (2012a) (450 ha) for example. Further experiments would need to cover a range of different reef formations in order to find out if there is a 'reef effect' as hypothesised in this study.

The average biodeposition rate per mussel, calculated by finding the difference between the live and dead *M. modiolus* treatments, was slightly lower than expected at 4.92mg mussel $^{-1}$ day $^{-1}$. To this day, the only other measurements of *M. modiolus* deposition known were made by Navarro and Thompson (1997) in flow through chambers during the spring bloom. At the peak of the spring bloom, the maximum rate was 40.9 mg mussel $^{-1}$ day $^{-1}$, however, rates dropped to 4-8 mg mussel $^{-1}$ day $^{-1}$ at the end of the bloom. Our measurements were made in July and therefore not at the peak algae concentration, which is normally in May in Loch Linnhe (Overnell et al. 1995), and therefore correspond with the lower values measured by Navarro and Thompson (1997), which may be more representative of the average annual biodeposition rate.

Filter feeders provide a crucial link between pelagic and benthic ecosystems, transferring energy in the form of organic material through faeces production but also sequesting carbon and other nutrients into the seabed. As shown in this experiment,

M. modiolus are capable of significantly enhancing the flow of energy from the water column to the benthos, and this process acts as to control coastal turbidity levels (Zhou et al. 2006), which is highlighted as an important ecosystem service as a supporting service (Townsend et al. 2011).

Considering that individual bivalves have the ability to filter substantial volumes of water, it is expected that when scaled up from an individual level to a reef level, the overall reef habitat will have a significant effect on the pelagic system. This has been demonstrated by Widdows et al. (2009) who found that mussel assemblages cause large scale clearance of particles from the water column. *M. modiolus* can occur in densities of up to 600 mussels per m^2 (Rees et al. 2008) and these reef formations cover over 370 ha (Lindenbaum et al. 2008), which implies that such reefs have a significant influence on the wider ecosystem.

Although the present study was only carried out on one small reef and over one week, the measurements of enhanced deposition due to biodeposition are in agreement with those measured by Navarro and Thompson (1997) outside the plankton bloom. The present experiment was carried out in an almost entirely natural setting and therefore represents a more realistic feeding environment. When taking into account passive and active processes, *M. modiolus* enhance sediment deposition by 32.5mg per m^2, which, when scaled up to the entire reef, accounts for ~34 tons of sediment per year. Therefore a larger reef, such as the Pen Llŷn reef (Lindenbaum et al. 2008), would be expected to accumulate a substantial amount of sediment and this can be seen in the sub bottom profile data as an accretion of reef material over the underlying lag gravel (Figure 28). It must also be considered however, that higher flow rates may limit the height of the reef in this location.

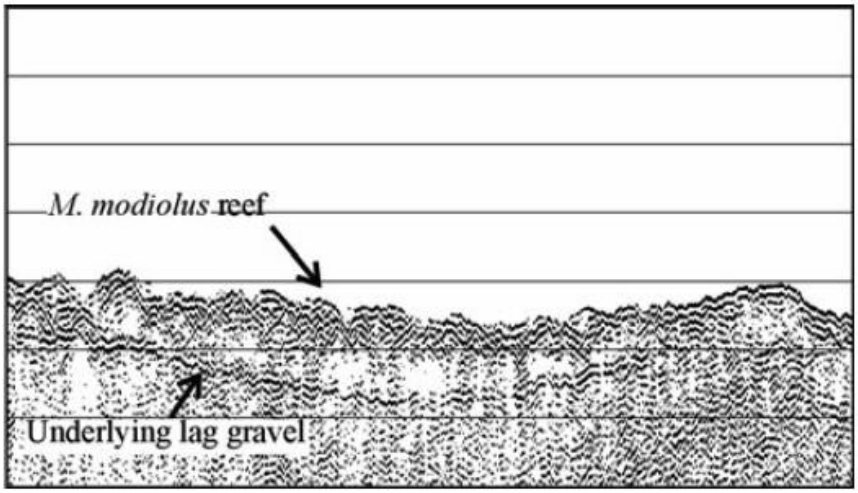

Figure 28. A profile image of the Pen Llŷn *M. modiolus* reef from (Lindenbaum et al. 2008) created using an IKB Seistec sub-bottom profiling system. Horizontal bars are 1.5m apart.

Granulometry samples collected from *M. modiolus* reefs in UVC transects in Chapter 2 show a high proportion of shell material in the sediment cores, and this is also reflected in the high $\delta^{13}C$ in the sediment samples collected in Orkney. Therefore, it is likely that a large amount of the material that accumulates on *M. modiolus* reefs is calcium carbonate, but there is an added accretion of carbon via biodeposits which become trapped between shells and buried into the reef structure. The organic and inorganic contribution to carbon sequestration must be considered together when investigating long-term carbon storage. The sedimentation experiment carried out in this chapter does not take into account the added accumulation from *M. modiolus* shells and the remains of associated fauna, which would probably increase our estimate by an order of magnitude. It is therefore expected that our measurements of reef accretion are an underestimation.

With wide scale loss of shellfish reefs including oyster reefs (Beck et al. 2011) and *M. modiolus* reefs (Bio-images 2007, Thurstan et al. 2013), it is likely that we have also experienced a decline in the associated ecosystem services provided by such habitats. Marine management measures should not only take into account the fisheries benefits of shellfish reef habitats (e.g. the nursery function), but also wider benefits such as carbon sequestration and bentho-pelagic coupling. Protection of highly valuable marine habitats can maintain the provision of ecosystem services to society.

Chapter 5. The effect of temperature on *Modiolus modiolus* biodeposition and byssus thread production

Abstract

Dense aggregations of *Modiolus modiolus* form biogenic reefs which provide ecosystem services to society, including bentho-pelagic coupling through active filtering processes. The maximum temperatures experienced by known *M. modiolus* reefs is 16 °C in the Irish Sea, although the species occurs as individuals further south where temperatures exceed those in the Irish Sea. Under controlled experimental conditions, *M. modiolus* were shown to respond to changes in seawater temperature by modifying their behaviour. In the short term (5 days), biodeposition rates decreased between 13°C and 15°C and in the long term (2 month acclimation), biodeposition rates were maintained between 10°C and 16°C but decreased at 19°C. In general, byssus thread production declined with increasing temperature and there was an interaction between *M. modiolus* biodeposition rate and sex. The implications of rising seawater temperatures for reef building organisms beyond those experienced at their biogeographical limit are discussed. This study demonstrates that understanding the mechanisms behind ecological functions is crucial if we are to determine how ecosystems may provide services in the future with predicted changes in environmental conditions.

Introduction

Modiolus modiolus reefs contribute to the provision of ecosystem services including providing an Essential Fish Habitat for shellfish (Chapter 2 and 3) and sediment sequestration (Chapter 4). In recent years, there has been increasing concern that over-exploitation of marine resources (Worm et al. 2006) and terrestrial resources (Schröter et al. 2005) has compromised Nature's resilience in supplying ecosystem services and benefits to society. In addition, climate change will undoubtedly modify natural processes and systems through increasing temperatures, extreme weather events and ocean acidification (Rhein et al. 2013). However, the impact of climate change on the provision of ecosystem services is unknown and it is likely that climate change may

have already affected some important underlying ecosystem functions (Schröter et al. 2005). Halting biodiversity loss should be a priority for policy makers (Worm et al. 2006) and deeper understanding of the biological processes that underpin ecosystems is required to manage the marine area effectively (Mooney et al. 2009).

Research has shown a poleward shift in populations of marine fauna over decadal timescales in response to gradual warming (Perry et al. 2005, Burrows et al. 2011), however, extreme climatic events have also been shown to structure populations (Smale and Wernberg 2013). Given that extreme climatic events are predicted to increase with climate change (Easterling et al. 2000) with more intense, longer lasting heat waves expected (Meehl and Tebaldi 2004), it is ever more important to understand how ecosystems and populations will respond to temperatures beyond their natural range. *M. modiolus* are widespread in the North East Atlantic although reef formations are rare and only remain in scattered locations (Rees 2009).

Temperature and food supply are important environmental drivers in bivalve behaviour (Bayne et al. 1993). Changes and rates of change in both of these can have profound effects on growth rates and condition (Honkoop and Beukema 1997, Rico-Villa et al. 2009). The section below provides detail on current understanding of how bivalves respond to changes in temperature and food concentrations.

Compared to terrestrial systems, the subtidal marine envornment is generally very stable in regard to its thermal conditions, thus even small changes in temperature can be highly stressful for a marine organism (Willmer et al. 2005). Environmental conditions drive evolutionary adaptation of species through natural selection, but on a short time scale, organisms can respond to environmental stressors by producing Heat Shock Proteins (HSPs), which act as ‘molecular chaperones’ to ensure that protiens do not unfold under stressful conditions (Somero and Hofmann 1997). Biological processes generally follow a biphasic response to temperature; the first phase involves an increase in the rate of activity due to the rate-enhancing effect of temperature, then during the second phase, the destructive effects of temperature take over and the rate of processes decline (see figure 8.9 in Willmer et al. 2005). This pattern is species specific and in general, the threshold temperature of HSP induction is related to the natural thermal envelope experienced by the species (Feder and Hofmann 1999, Jansen et al. 2007).

Lesser and Kruse (2004) found that *M. modiolus* respiration rates are significantly higher in the summer (15°C). During winter months, they are able to maintain metabolism by producing high concentrations of rate-limiting enzymes, suggesting that *M. modiolus* is a cold adapted species. However, the experimental temperatures covered by Lesser and Kruse (2004) did not go beyond the natural range for *M. modiolus*. Ezgeta-Balic et al. (2011) found that *Modiolus barbatus* only have enough energy for growth and reproduction for less than five months every year, based on clearance and respiration rates. Such physiological limitations in subtidal mussels would suggest that rising seawater temperatures could put pressure on these populations and the habitats that they create.

In marine filter feeders, the gill has a dual function as it is used for both feeding and respiration (Gosling 2003), therefore these behavioural attributes can be studied in combination with valve-gape activity (Riisgard et al. 2003). Studies have shown a positive trend in respiration and feeding rate with temperature for bivalves (e.g. *Musculista senhousia*: Inoue and Yamamuro 2000). According to Gosling (2003) clearance rate (for feeding) and filtration rate (for respiration) are controlled independently in bivalves and research has shown that respiration rates can differ greatly from feeding rates. For example, Järnegren and Altin (2006), report very low respiration rates in *Acesta excavata* (0.12ml O_2 $h^{-1}g^{-1}$) along with high feeding rates.

It is important to consider the natural environment of a species when interpreting thermal tolerances derived from laboratory experiments. For example, Loayza-Muro and Elías-Letts (2007) found that *Anodonites trapesialis*, the tropical freshwater mussel, feeds 80% faster at 20°C compared to 5°C. Conversely, clearance rates in the Arctic bivalve, *Hiatella arctica* increased between 0 and 15°C, then declined to minimal rates between 15 and 25°C (Petersen et al. 2003). Savina and Pouvreau (2004) found no impact of temperature on feeding rate of *Glycymeris glycymeris* or *Paphia rhomboides*. Although interestignly, the long lived, slow growing species *G. glycymeris* showed low feeding rates that were independent of phytoplankton concentration, whereas *P. rhomboides* feeding rate was much higher than *G. glycymeris* and increased with increasing food concentration. This indicates that short lived species need to respond quickly to changes in local food concentrations in order to make the most of the avaiable food when they can.

M. modiolus is an Arctic-boreal species and their distribution range from Iceland to the Bay of Biscay (Rees 2009). Figure 1 (chapter 1) shows the known location of *M. modiolus* beds from a review of documented records by Gormley (2013), with the southernmost bed located in the Irish Sea. Here, the seawater temperatures range from 6 -16 °C (see appendix D2), whereas, populations from New Hampshire experience a temperature range of 5-15°C (Lesser and Kruse 2004) and those sampled from Noway experience temperatures as low as 2°C and only reach 8°C in the summer (Brown 1984).

When investigating the thermal tolerance of marine molluscs it is important to take into account the amount of time that an animal has been able to acclimatise to the experimental conditions. The acclimation periods used in thermal tolerance studies vary from none (e.g. Abele et al. 2001), 7 days (Ezgeta-Balic et al. 2011), 10 days (Jiang et al. 2006), and 6 weeks (Buckley et al. 2001) and the lethal thermal limits reported for bivalves varies with acclimation time (Zippay 2012). In general, the minimum acclimation duration used in the majority of experiments is 2 weeks (Lei et al. 1996, Anestis et al. 2007, Young 1985).

As well as respiration and feeding behaviour, other important physiological functions are affected by temperature, for example Brodsky et al. (2011) found lower byssal thread production in *Mytella charruana* and *Geukensia demissa* when exposed to temperatures close to their lethal thermal limit (10°C and 13°C respectively). Young (1985) found that byssus thread production in *Mytilus edulis* increased with increasing temperatures up to 25°C, however, agitation was the most important factor affecting byssus thread production. In fact, it seems that byssus thread production in bivalves is highly sensetive to a number of factors including temperature and flow rate (Archambault et al. 2013).

In order to investigate the functional response of *M. modiolus* at maximum temperatures experienced in the wild, experiments were carried out under controlled conditions using Vortex Resuspension Tanks (VoRTs) (Davies et al. 2009). Biodeposition rate (faeces and pseudofaeces production) and byssus thread production of individual mussels are used as a measure of ecosystem function (e.g. chapter 4). A short-term experiment (5 days) will examine the impact of sudden changes in temperature, whilst acclimation of

M. modiolus will be used to investigate the long-term effects of temperature on *M. modiolus.*

The experiments presented here test the following hypotheses: 1) *M. modiolus* biodeposition rate decreases when exposed to seawater temperatures greater than the thermal maximum experienced in the wild for 5 days. 2) After an acclimation period, *M. modiolus* biodeposition rate and byssus thread production decrease with increased seawater temperature. The intention of testing the above hypotheses is to investigate the response of *M. modiolus* to changes in temperature in the context of extreme weather events and persistent changes in the subtidal marine environment as predicted by the IPCC (2014). For each experiment, *M. modiolus* are held at biogeographically relevant temperatures based on seawater temperatures measured on horse mussel reefs at or nearby the sampling location.

Methods

Environmental Parameters

Benthic seawater temperature was monitored at two reef sites using temperature loggers. On the *M. modiolus* reef in the Irish Sea, a Vemco minilog II (calibrated accuracy ±0.1°C from 5°C to 35°C) was used to record daily seawater temperature for 5 years (redeployed yearly by SCUBA divers) and a Hydrolab MS5 minisondes (±0.01°C) was deployed on a *M. modiolus* reef in Loch Creran on the west coast of Scotland for 9 months. This *in situ* data was used to determine the experimental temperatures used in the aquarium experiments.

In order to estimate the amount of food available for *M. modiolus* in summer in Loch Linnhe, three 1 litre water samples were taken in July 2014 from Port Appin at high tide. The water was filtered on a Whatman GF/C glassfibre filter (1.2µm retention), dried and weighed to give the total dry weight of organic and inorganic material suspended in the water. In addition to this, long term phytoplankton data collected by Greg Moschonas at SAMS in Loch Linnhe was used to determine the natural algae concentrations during July (approx. 500 cells per ml or chlorophyll concentrations of 7µg l^{-1}).

Aquarium Experiments

Three experiments were carried out in the aquarium; a short-term experiment with no acclimation period (Experiment 1) and two long-term experiments (Experiments 2 and 3). In Experiment 2, food was limited but in Experiment 3, food concentrations were approximately at summer levels. The details of the experiments carried out in this chapter are outlined in Table 5, while table 6 shows a summary of the different food conditions in each aquarium experiment. Food concentrations are given as TPM measurements taken directly from the VoRTs in comparison to *in situ* measurements taken in July 2014 from Loch Linnhe.

Table 5. Acclimation periods for each experiment and treatments used. Total Particulate Matter (TPM) of the VoRT water is given to show the food available during the experimental period (not including acclimation), CI = Condition Index.

Experiment	**Acclimation**	**Treatments (n=no. VoRTs used)**	**TPM (mg l^{-1})**	**Observation Duration**	**Hypothesis and response**
Experiment 1	None	13°C and 15°C, n=5	2.69	5 days	H_1 - Biodeposition
Experiment 2	1 month	13°C, 16°C and 18°C, n=4	0.80	7 days	H_2 - Biodeposition and byssus
Experiment 3	2 months	10°C, 13°C, 16°C and 18°C, n=3	3.32	7 days	H_2 - Biodeposition, byssus and CI

The VoRTs were on an open, flow through system (20 litres per hour) with a pump maintaining a circulatory flow and an uplift providing resuspension of food and inorganic material so that the tank remained well mixed throughout the experiments. Heating elements were used in combination with a thermostat to set each VoRT to the desired temperature. The VoRTs were maintained under a consistent 12 hours light:12 hours dark (LD12:12) photoperiod throughout each experiment to mimic the conditions experienced during collection around the autumn equinox.

Table 6. Total Particulate Matter (mg dry weight l^{-1}) from water samples taken from natural seawater as a guide for recreating food concentrations (organic and inorganic material) in the VoRT experiments (1-3) supplied with Shellfish Diet 1800. Averages given for each sampling period ± 1SE.

Seawater TPM	**VoRT water TPM**		
Loch Linnhe	**Exp 1**	**Exp 2**	**Exp 3**
4.8	2.87	1.34	2.93
5.1	1.44	0.58	3.40
1.9	3.75	0.81	2.03
		0.49	3.33
			2.60
			5.60
3.93 ± 1.02	**2.69 ± 0.67**	**0.80 ± 0.19**	**3.32 ± 0.50**

M. modiolus were fed Instant Algae Shellfish Diet 1800: an aquaculture feed for oysters, mussels and scallops which contains four marine algae, *Thalassiosira weissflogii* (20%), *Tetraselmis* (25%), *Pavlova* (15%) and *Isochrysis* (40%). Although the algae are dead, the mixture of cell types provides a more nutritional diet compared to a single cell culture, and it is easier to maintain a constant concentration of food. The artificial food was diluted into a 200 litre stock tank, and this was distributed to the VoRTs using a peristaltic dosing pump (Watson-Marlow 205S/CA manual control 12-channel cassette pump) at 60ml hr^{-1}. Using a large stock volume and a peristaltic pump ensured that all replicate VoRTs were supplied the same volume and concentration of food at a constant rate throughout the experiment.

For all experiments, *M. modiolus* were starved for 1 week prior to starting the experiment to ensure the guts were empty at the start of the experiment in order to measure a feeding response during the controlled experiment. Throughout each experiment, the amount of food available for the mussels was monitored either with turbidity, fluorescence or TPM (mg dry wt. l^{-1}) measurements (or a combination of all three) taken from the VoRT water.

Turbidity and fluorescence were measured daily as these provided an immediate measure of the food concentration that could be easily monitored for the duration of the experiment. TPM and chlorophyll measurements were also taken and calibrated with turbidity and fluorescence respectively, however these samples required at least 24 hours for processing before results could be obtained. Environmental parameters in the aquarium (turbidity, fluorescence and conductivity) are shown in Appendix D4 – D9.

For each experiment, epifauna were carefully removed from the live mussel shells and the length of each mussel was recorded. Control mussels were also cleaned and epifauna removed. Large *M. modiolus* (>98cm) were placed in 15cm long pipe sealed at the bottom with a Petri dish to contain the biodeposits. Smaller mussels (<98cm long) were placed in shorter pipe (9.7cm long) with the same diameter as the long pipe (8.9cm), see Figure 28 A, to ensure approximately the same mussel length : container volume ratio. Control mussels were made using cement to hold together *M. modiolus* shells and these were also placed into chambers and into the VoRTs to account for passive deposition attributable to the physical structures.

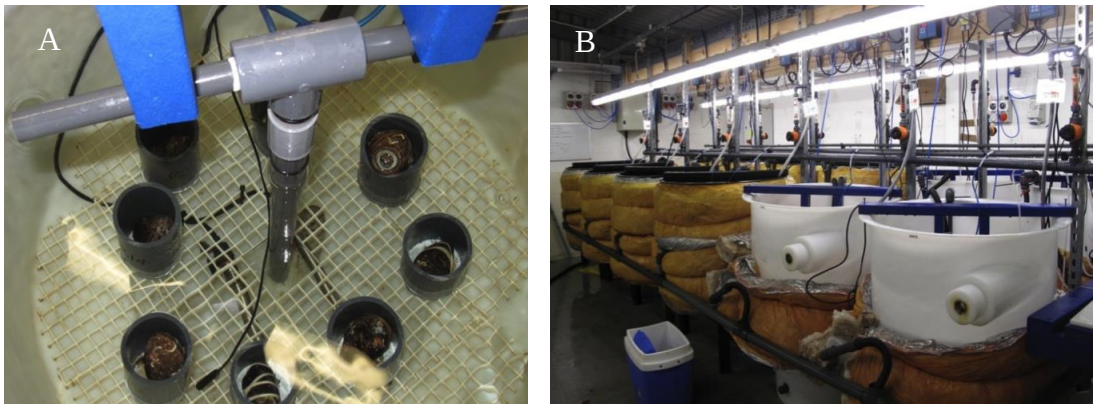

Figure 28. Images showing the chambers used to hold the live *M. modiolus* and controls (A) and the VoRT set up (B).

Live mussel chambers and control chambers were placed in a random order in the VoRTs to account for potential spatial variability of particle deposition within the VoRTs. According to Davies et al. (2009), water velocity decreases towards the centre of the VoRT, which can influence particle settlement. Although inorganic sediment was

not used in the present study, concentrated algae were added to the VoRTs, and it was important that the amount of food available was relatively consistent between mussels. The size-frequency of *M. modiolus* chosen were balanced between experimental treatments.

Measurements of biodeposition were taken as follows: At the start of each experiment, *M. modiolus* were cleaned before placing into their individual chambers and into the VoRTs. At the end of the experiment the chambers were carefully removed from the VoRTs and the *M. modiolus* were cleaned again. The water from the washed mussels and the water from individual mussel chambers was retained in a labelled sample pots. Any biodeposits remaining in the chambers were also washed into the sample using a wash bottle. The water samples were then filtered on pre-dried Whatman GF/C filters following Navarro and Thompson (1997) and washed through with distilled water to remove salt. The filters were dried at 100°C until they reached a constant weight. The weight of the filter was then subtracted from the final weight to give the Total Particulate Matter (TPM) for each sample. The TPM collected in the control chambers was subtracted from the sediment deposited by live *M. modiolus* to give a biodeposition rate. For Experiment 2 and Experiment 3 byssus threads were cut before and after the observation period. The byssus threads collected at the end of the experiments were dried and weighed to measure byssus thread production.

Experiment 1: The effect of short-term temperature change on M. modiolus function at their summer maximum temperature

Seventy *M. modiolus* were collected from the Port Appin reef in Loch Linnhe on the west coast of Scotland on the 22/09/2012 during a drift dive starting at 56° 33’ 1.8’’ N, 5° 25’ 26.4’’ W drifting in a south-westerly direction for approximately 200m. VoRTs were set up with 40 live mussels and 40 control mussels randomly assigned to each VoRT. The size distribution of *M. modiolus* used in this experiment are shown in appendix D1, where the size range was selected to represent the adult *M. modiolus* population on the Port Appin reef.

The temperature treatments were chosen based on temperature data from Loch Creran, which reached a maximum of 14.09°C and an average summer temperature of 12.99°C in 2013 (appendix D3). In order to simulate a summer extreme temperature, 15°C was chosen as the high temperature treatment and this was compared to the ambient

aquarium temperature (approximately 13°C). Four replicate tanks were used for each temperature treatment and the treatments were randomly assigned to the VoRTs. As well as turbidity, temperature and flow rate were monitored two to four times a day for five days. *M. modiolus* were not acclimated prior to the start of this experiment although the water temperature was raised to the target temperature over 5 hours.

Experiment 2: The long-term effect of biogeographical relevant temperature change on M. modiolus function with low food concentrations

In December 2013 *M. modiolus* were collected from Scapa Flow, Orkney, Northern Scotland at 58° 53.307N, 003° 10.575W. Of these, 36 were selected with a shell length between 96mm and 120mm. *M. modiolus* were fed 5ml Shellfish Diet once a week during the 1 month acclimation period and during the 7 day experiment, dilution of the concentrated algae feed was calculated to meet the target concentration (500 cells per ml) in the VoRTs. For this pilot study, three temperature treatments were used: 13°C; 16°C; and 18°C with four replicate VoRTs used for each treatment.

Experiment 3: The long-term effect of biogeographical relevant temperature change on M. modiolus function with summer food concentrations

For Experiment 3, 100 *M. modiolus* were collected from the Port Appin *M. modiolus* reef in Loch Linnhe at 56° 33’ 1.8’’ N, 005° 25’ 26.4’’ W on the 07/09/2014. All mussels were kept at the aquarium with a natural seawater supply (although filtered through sand), maintained at 15°C and fed 5ml once a week using Shellfish Diet 1800.

On the 09/12/2014, 23 *M. modiolus* were transferred into a 13°C acclimation tank whilst 46 were transferred to 16°C. A further 23 were transferred to ambient temperature (~11°C). In order to achieve a gradual increase in temperature on the 18/12/2014, 23 *M. modiolus* were transferred from the 16°C acclimation tank to a 19°C tank. For all transfers, *M. modiolus* were added to new tanks within water from original tank to reduce shock. The temperatures used in this experiment were chosen to show the functional response of *M. modiolus* at the thermal maximum experienced in the wild as a reef formation (see appendix D2: 16°C on the Pen Llŷn reef) and as individuals (Bay of Biscay 20°C maximum: Koutsikopoulos et al. 1998). The acclimation periods were chosen as to mimic but not exceed the rate of temperature change experienced by *M. modiolus* in the wild.

After the acclimation period, *M. modiolus* were transferred to the VoRTs which were set to either 10°C, 13°C, 16°C or 19°C; with three replicate VoRTs per treatment. The temperature treatments were randomly assigned to the 12 VoRTs using a randomized block design. For seven days food supply, flow rate and temperature were monitored. The target food concentration was 7µg Chl a l^{-1} or 3.9mg TPM l^{-1} based on field measurements (see Table 6). This food concentration was chosen to represent the natural food available in Loch Linnhe in July 2012 in order to relate this data to the *in situ* measurements described in Chapter 3. Fluorescence measurements were calibrated with chlorophyll extractions from the VoRT water to monitor the food concentrations throughout the experiment (Appendix D10 and D11). Fluctuations in temperature and salinity are known to affect fluorescence readings (Carstea 2012), therefore conductivity of the seawater inflow was monitored throughout the experiment also.

At the end of the 7 day experiment, all biodeposits were collected from 3 *M. modiolus* from each VoRT and the byssus were cut, dried and weighed. The mussels were then dissected to determine the sex following Dinesen and Morton (2014) and considered to be male if the gonads were yellow (see Figure 29 A) and female if the gonads were an orange colour (Figure 29 B).

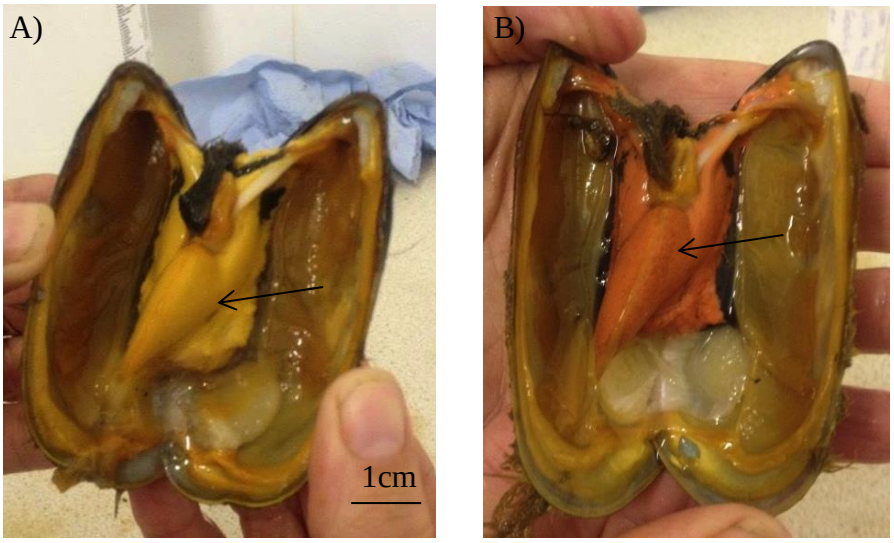

Figure 29. A) Male *M. modiolus* with yellow gonad and B) female *M. modiolus* with orange gonad. Arrows shows the location of the gonad. Image: Flora Kent.

Condition Index

Ten *M. modiolus* were frozen before the acclimation period for Condition Index. At the end of Experiment 3, eight *M. modiolus* from each treatment were also taken for Condition Index. The condition of the mussels used in the experiment was measured to ensure that food was not limited throughout the experiment. The height, length and width of the mussels were measured and the soft tissue dried at 70°C, then the soft tissue and shells were weighed. The ratio of dry tissue weight : dry shell weight was multiplied by 100 to obtain a condition index for the mussels (after Mladineo et al. 2007).

Data Analysis

In Experiment 1 the average sediment collected in the control chambers was subtracted from the average sediment deposited by each live *M. modiolus* in each VoRT to give an average active biodeposition measure for each VoRT. An ANOVA was used to test whether the deposition by *M. modiolus* in the 15°C VoRTs was different to that deposited by *M. modiolus* in the 13°C VoRTs.

For Experiment 2 and 3, biodeposition was calculated for each individual *M. modiolus* by subtracting the average background deposition in each VoRT (the control mussels) from the deposition by each live *M. modiolus*. Response data were assessed for overall distribution and where necessary log transformed. A general linear mixed model was used to test the response variable 'biodeposition' with 'temperature' and 'sex' as fixed factors. VoRT number was included as a random factor following Zuur et al. (2009), using the 'lme4' package in R (Bates et al. 2011). Akaike's information criterion (AIC) values were checked between models and a Likelihood Ratio Test used to find the model with the best fit.

Byssus weight data from individual *M. modiolus* at the different temperatures were compared using a general linear mixed model with VoRT number as a source of random variance. The inclusion of a random component in the analysis required the use of a mixed model to account for inherent differences between VoRTs (Millar and Anderson 2004). Condition Index data were normally distributed (Anderson Darling test) and homoscedastic (Levene's test). A two way ANOVA was used to compare the condition of *M. modiolus* held at different temperatures using 'temperature' and 'sex' as

fixed factors. All statistical tests were carried out in R (R Development Core Team 2011).

Results

Experiment 1: The effect of short-term temperature change on M. modiolus function at their summer maximum temperature

A regression analysis showed a weak positive relationship between *M. modiolus* size and biodeposition rate, however, this was not significant ($R^2 = 0.07$, p=0.23). The biodeposition rate of *M. modiolus* held at 13°C for five days was significantly higher than those at 15°C (ANOVA, p=0.03; Figure 31). It was also noted that three of the *M. modiolus* in the 15°C treatment were not attached to their individual chambers at the end of the experiment, whereas all other *M. modiolus* were attached to their experimental chambers and required cutting free.

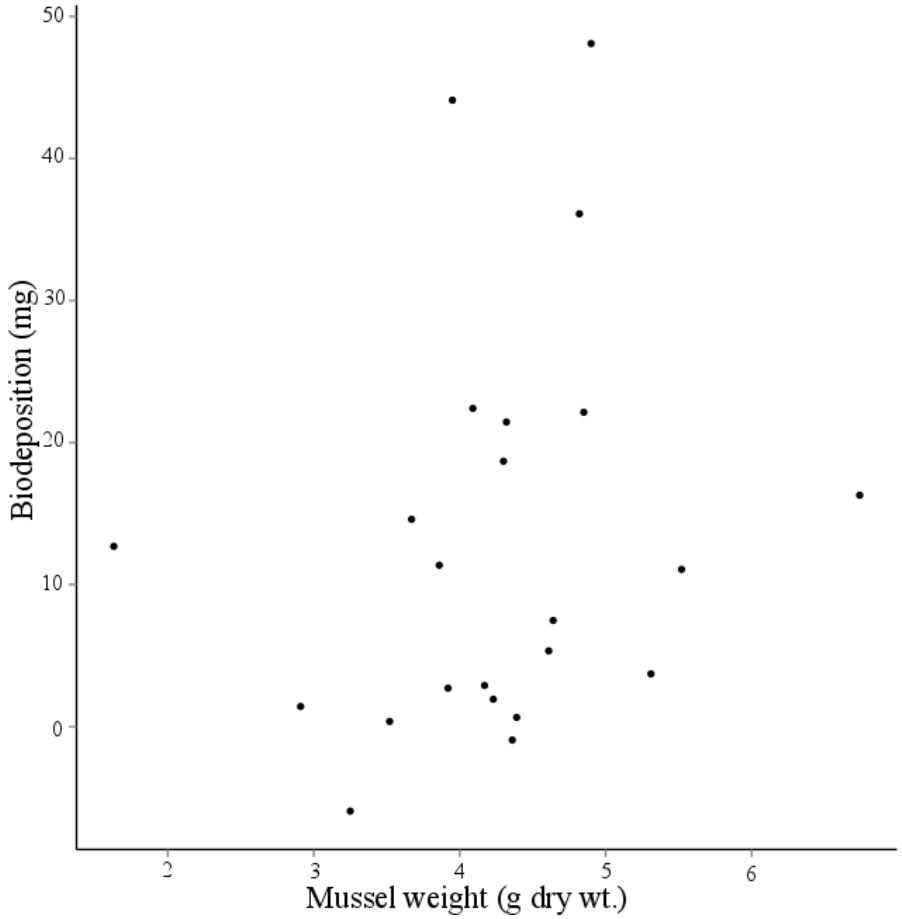

Figure 30. Biodeposition for individual *M. modiolus* held in VoRTs at 13-15° C for 5 days supplied with 2.69mg dry weight shellfish food per litre.

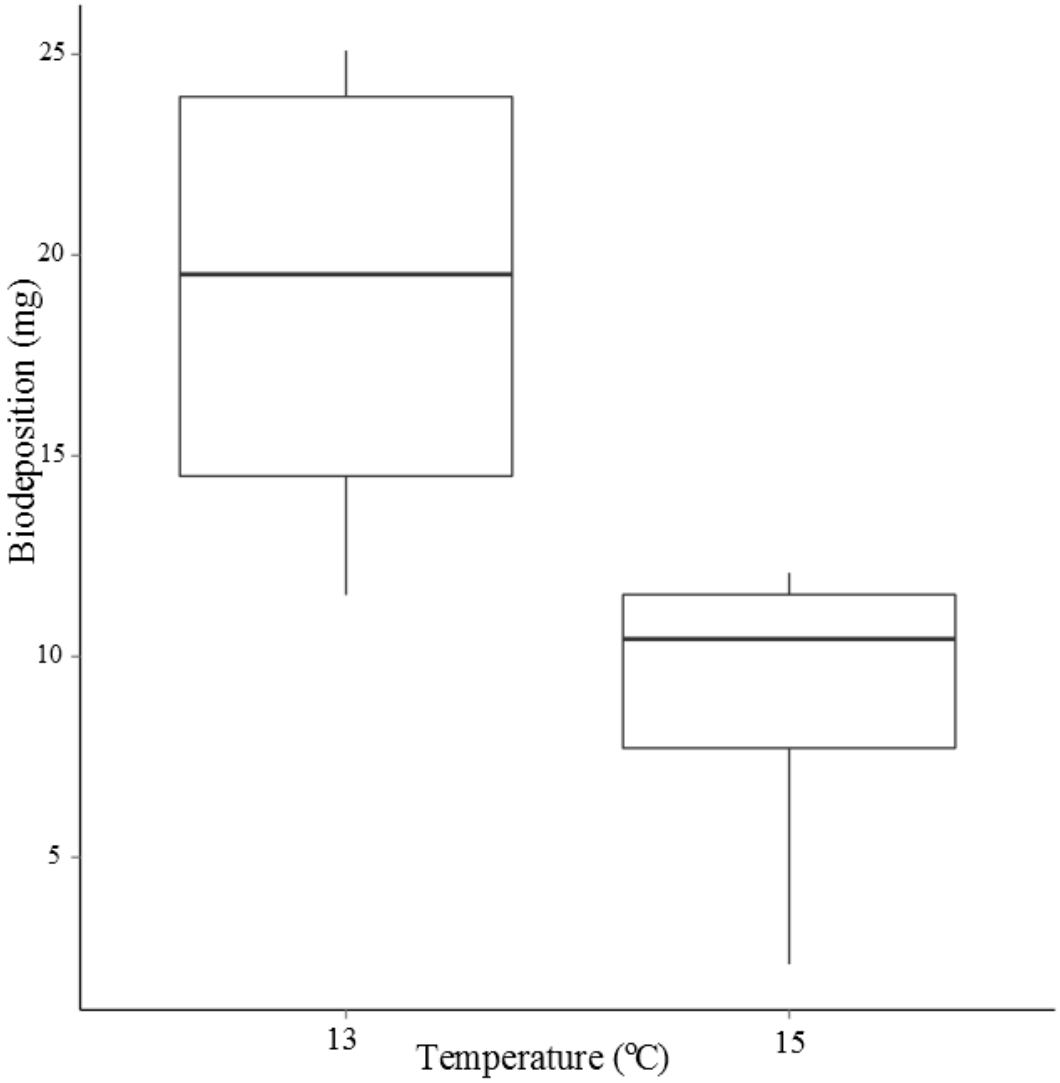

Figure 31. *M. modiolus* biodeposition rate at two temperatures with no acclimation, data shows average deposition per VoRT minus background deposition (n=4) over five days (Experiment 1).

Experiment 2: The long-term effect of biogeographical relevant temperature change on M. modiolus function with low food concentrations

Less faeces and pseudofaeces were produced in Experiment 2 compared to Experiment 1 (between 0 and 100 for trial 1 and between 0 and 25 for trial 2), and biodeposition was not significantly influenced by temperature (general linear mixed model, p=0.17). Higher seawater temperature had a negative effect on byssus thread production; illustrated in Figure 33. Temperature was a significant influence on byssus production overall (ANOVA; F =5.82, p=0.024); the weight of byssus thread material was significantly higher at the lowest temperature (13°C) than the highest temperature treatment (18°C) (Tukey post hoc test, p=0.019).

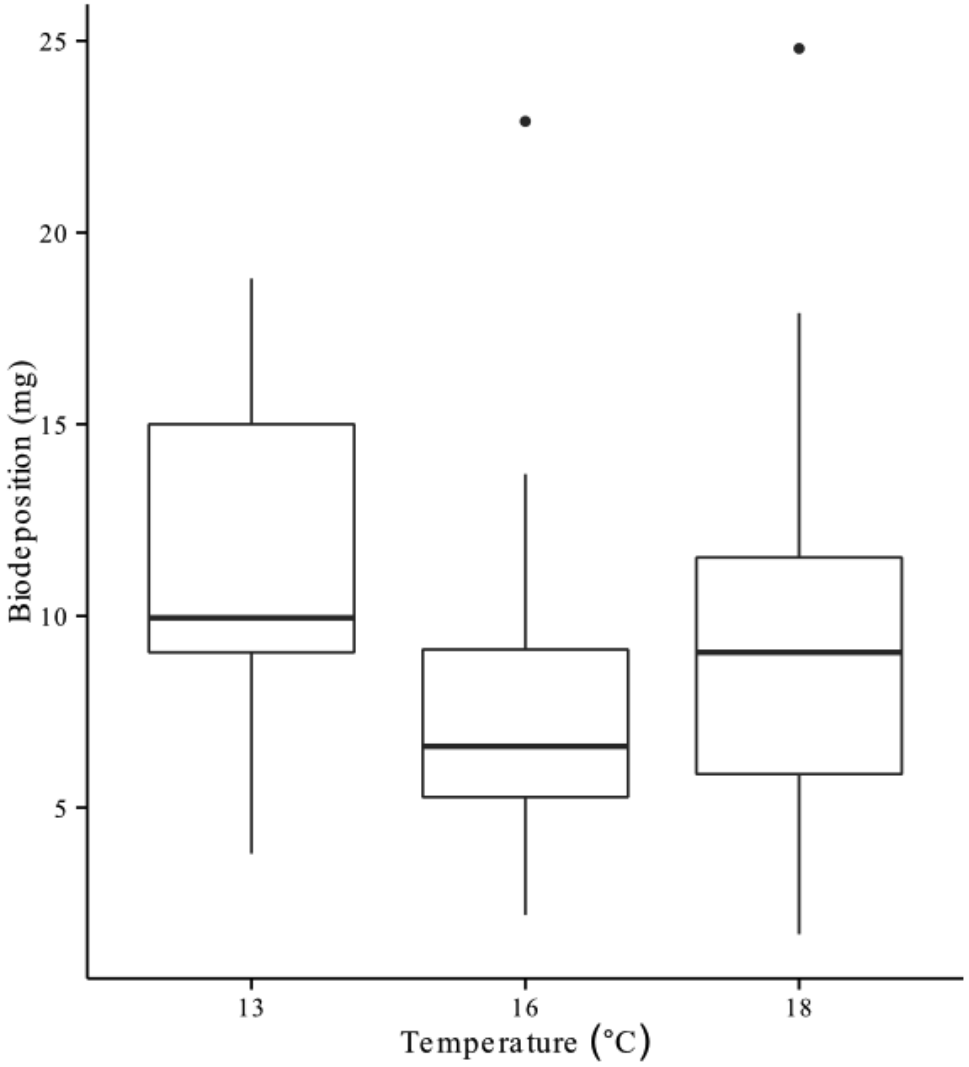

Figure 32. *M. modiolus* biodeposition rate during Experiment 2 over seven days with 12 *M. modiolus* at each temperature treatment (n=12) and 1 month acclimation.

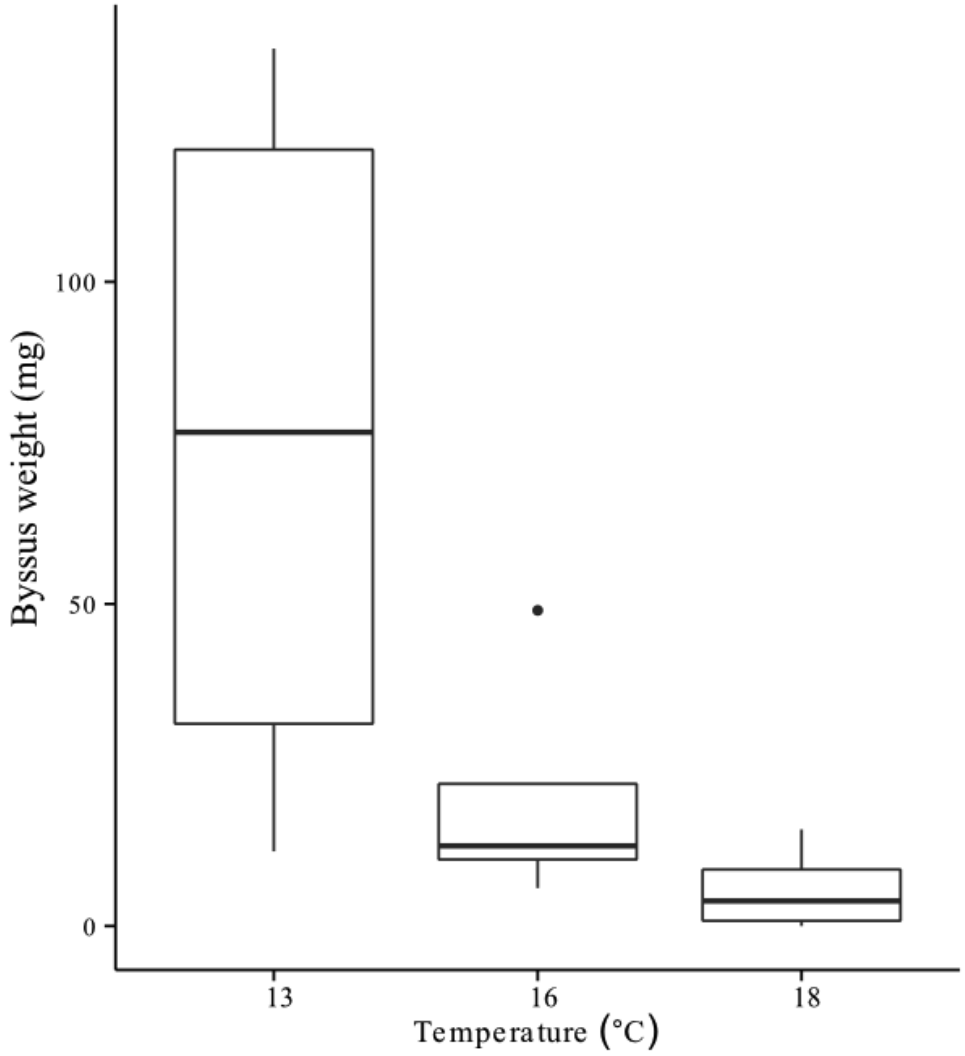

Figure 33. *M. modiolus* byssus thread production after seven days at three temperatures with 1 month acclimation. Samples reflect the weight of byssus thread for each VoRT (n=4) from Experiment 2.

Experiment 3: The long-term effect of biogeographical relevant temperature change on M. modiolus function with summer food concentrations

The highest biodeposition rate during Experiment 3, was 4mg day^{-1} for a single *M. modiolus* in a 10 °C treatment and the lowest biodeposition rate was 1.55mg day^{-1}, which was from a 19 °C treatment. Over the 7 day experiment, biodeposition by *M. modiolus* was high in the 10°C, 13°C and 16°C treatments (45.08mg at 16°C, for example) and dropped to approximately half this (20.18mg) in the 19°C temperature treatment. Biodeposition was significantly affected by temperature (p=<0.015) and although 'sex' was not significant (p=0.609), the interaction between temperature and sex was significant (p=0.035). Figure 34 shows the different response between male and

female *M. modiolus* in regard to biodeposition. Male *M. modiolus* have a high biodeposition at low temperatures (10-13°C), and this drops from 57mg at13°C to 39mg at 16°C and 20mg at 19°C. On the other hand, biodeposition in female *M. modiolus* is low at 10°C (21mg) and reaches a maximum (56mg) at 16°C.

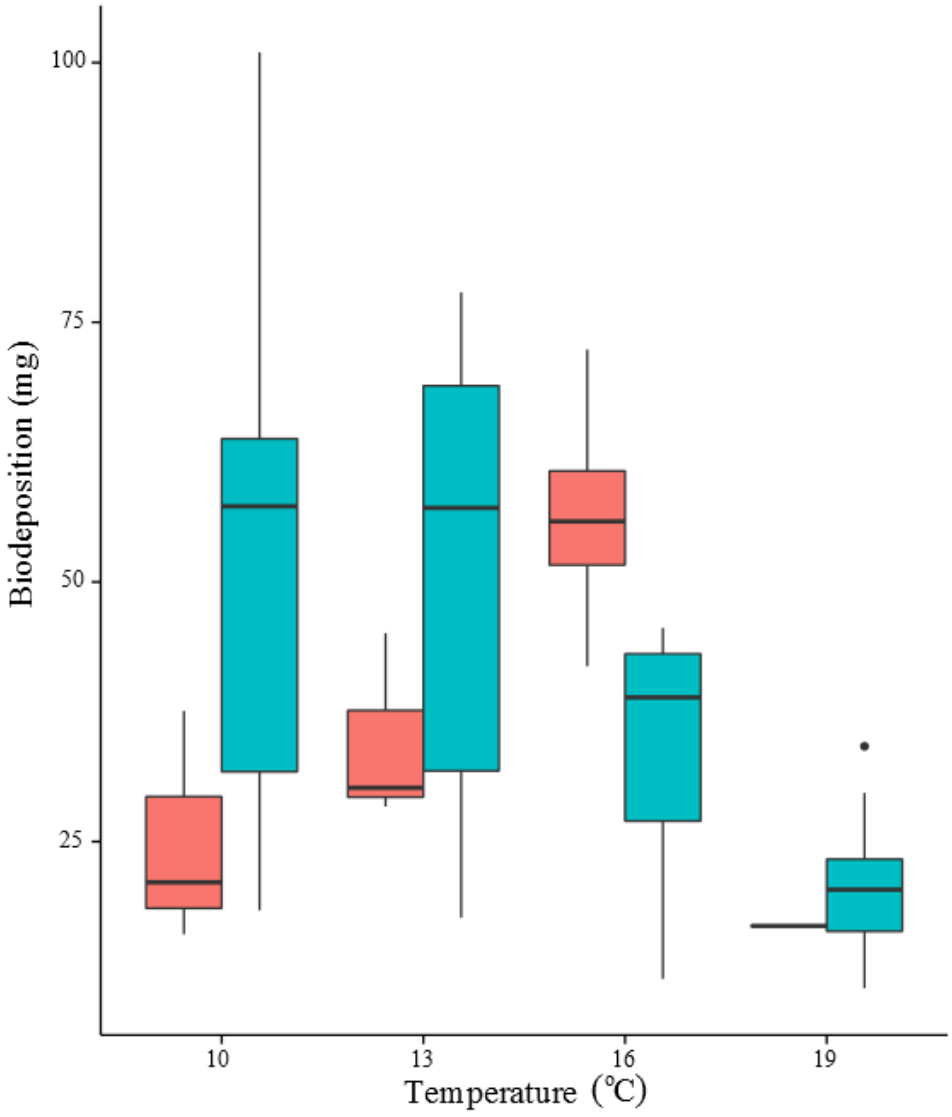

Figure 34. *M. modiolus* biodeposition over seven days at four temperatures with two months acclimation (Experiment 3). Box plots show males (blue) and females (orange).

At the end of the Experiment 3 all *M. modiolus* were attached to their containers apart from 8 individuals. Four of these were in a 19°C treatment, two were in 16°C treatments and the remaining two were in a 13 and 10°C treatment. One *M. modiolus* had no byssus at all and this was in a 16°C VoRT.

A negative trend of byssus thread production with temperature was displayed in Experiment 3, although this was not as clear as seen in Experiment 2. Temperature was a significant factor in Experiment 2 ($p=0.04$) and the weight of byssus produced was more variable at lower temperatures both Experiment 2 and Experiment 3 (the 10°C and 13°C compared to 16 and 19°C; Figure 35). The most noticeable drop in byssus production occurs between 13°C and 16°C (see Figure 33 and 35).

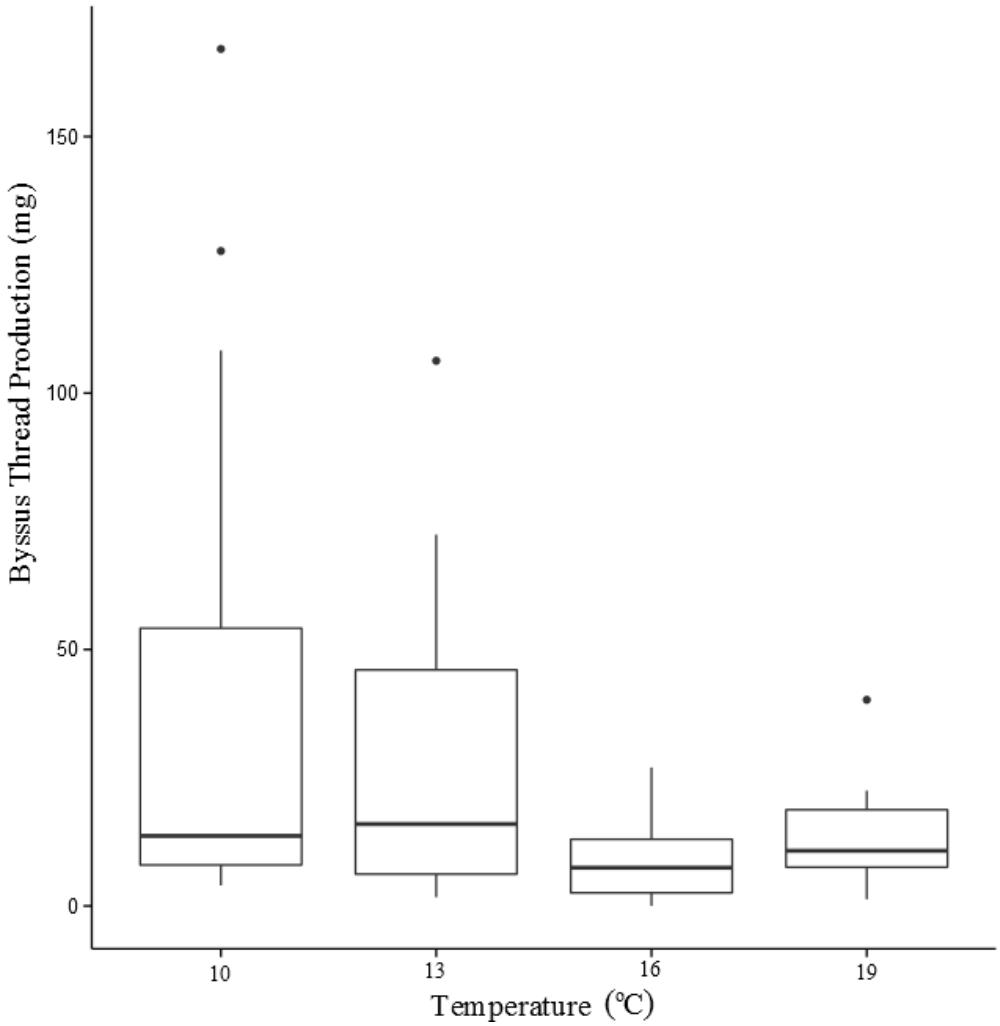

Figure 35. *M. modiolus* byssus thread production after seven days at four temperature treatments from nine individuals per treatment with two months acclimation (Experiment 3).

The flesh dry weight of mussels used in Experiment 3 showed a stronger correlation with shell dry weight than flesh wet weight (R^2 = 0.45 and R^2 0.30 respectively), therefore the ratio between flesh dry weight and shell dry weight was used to calculate Condition Index (CI) of the 3 shell measurements taken (length, width and height), shell width showed the strongest correlation with flesh dry weight (R^2=0.19, p=0.09). Neither biodeposition rate or byssus thread production showed a significant correlation with flesh dry weight (R^2=0.03, p=0.28 and R^2=-0.10, p=0.87 respectively). CI was slightly higher in *M. modiolus* samples taken before the acclimation period compared to those taken at the end of the experiment (8.4% and 7.7% respectively), however this was not significant (F=1.8, p=0.17).

Interestingly, the CI of *M. modiolus* held at the different experimental temperatures follows a similar pattern to the different biodeposition rates at these temperatures (see Figure 36 and 34). The CI generally increased with temperature, reaching a maximum at 16°C (8.25%), then dropped in the *M. modiolus* from the 19°C treatment to 8%, although the difference is subtle and temperature was not a significant factor (F=0.68, p=0.57). No direct correlation was seen between biodeposition rate and CI (-0.09, p=0.76). Figure 37 shows that the low condition of the 10°C *M. modiolus* was driven by a drop in body weight to shell weight ratio of male *M. modiolus* to 6%. Female *M. modiolus* show a consistently higher CI than males, however, this is most pronounced at the lowest temperature tested in this experiment.

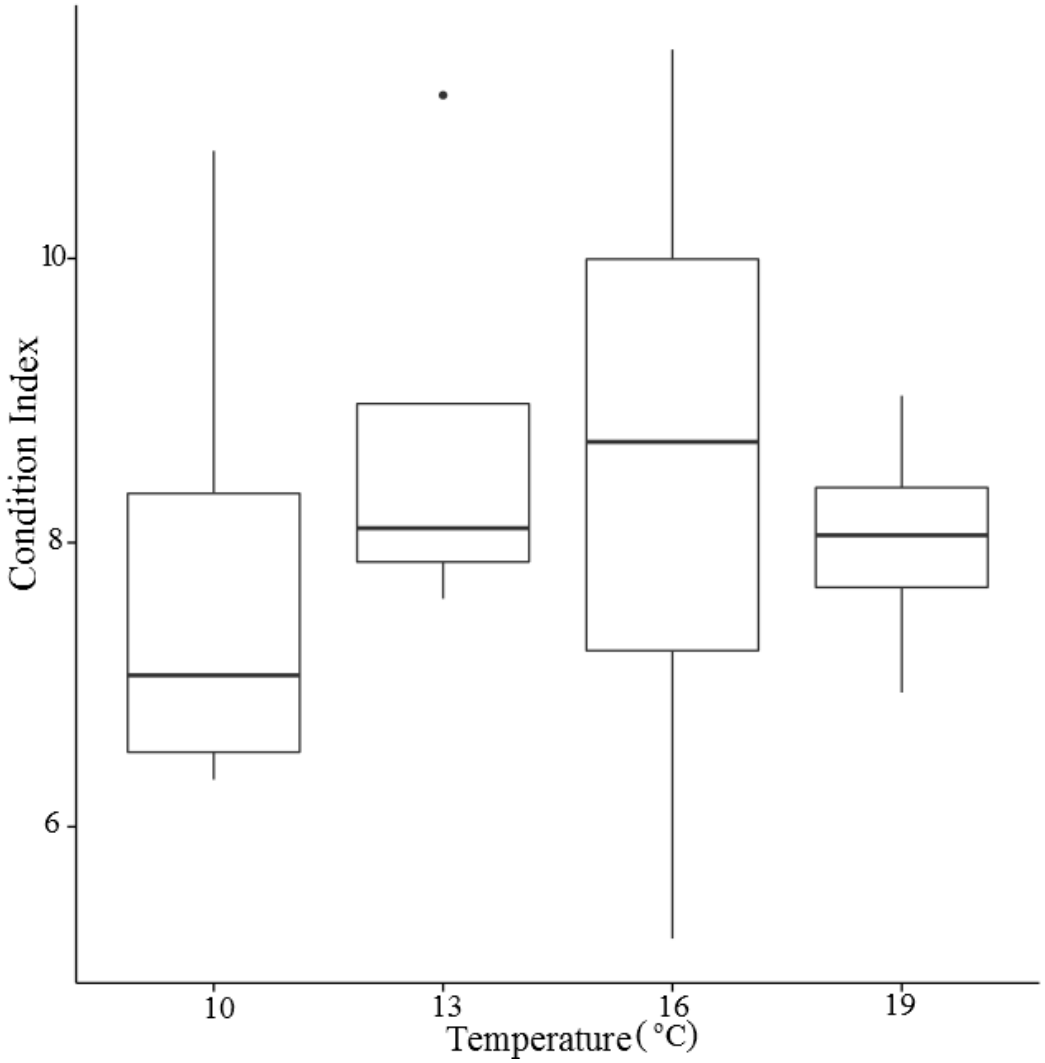

Figure 36. *M. modiolus* Condition Index (flesh dry wt. : shell dry wt.) at four temperatures (n=8 for each temperature treatment) held in aquarium tanks for 5 months with a constant supply of shellfish food.

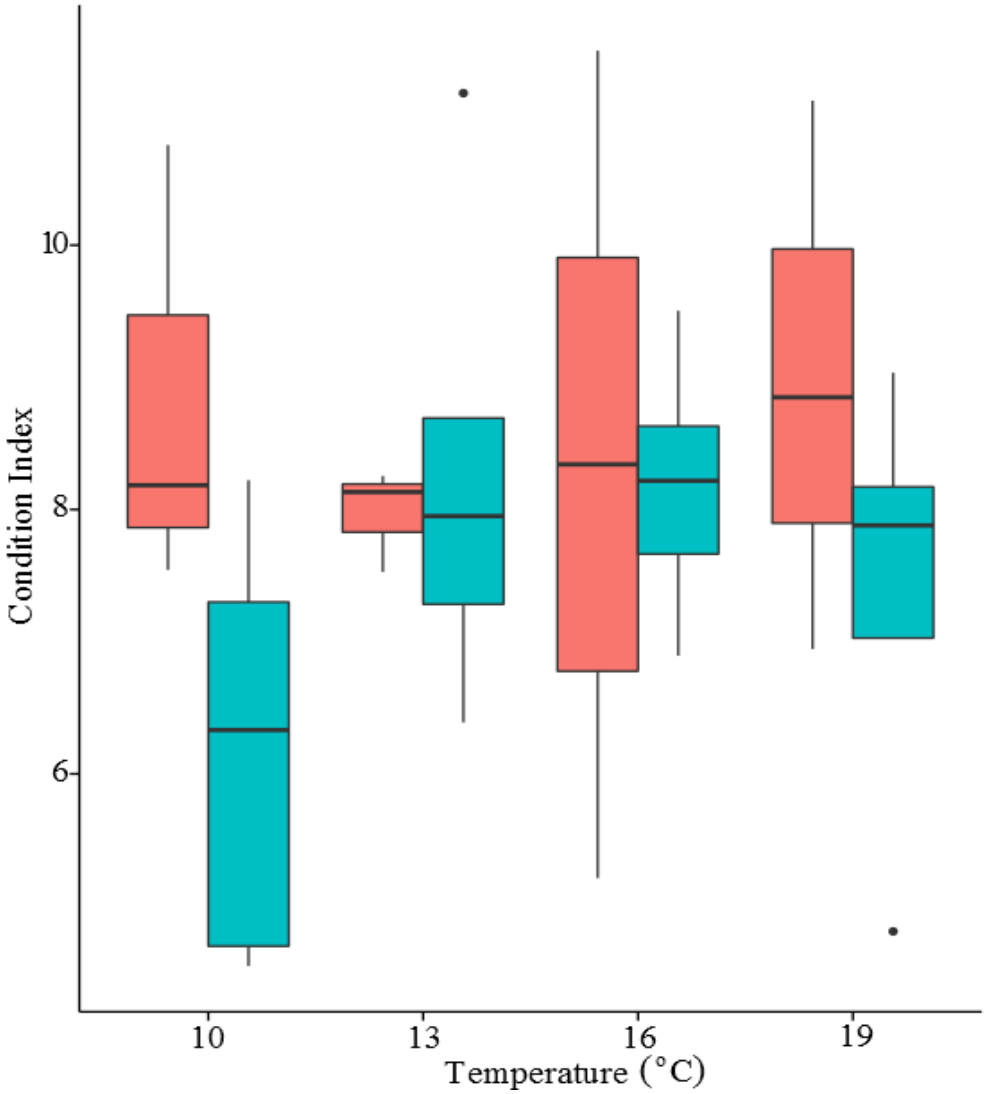

Figure 37. Male and female *M. modiolus* Condition Index (flesh dry wt. : shell dry wt.) at four temperatures. Box plots show males (blue) and females (orange) held in aquarium tanks for 5 months with a constant supply of shellfish food.

Discussion

The aim of this chapter was to investigate the impact of temperature on *M. modiolus*, which was successfully accomplished using VoRTs. The advantage of using this system was that algae concentrations were maintained within the VoRTs and the peristaltic pump allowed a constant and equal supply of food to each VoRT. The experiments presented here demonstrate that the *M. modiolus* respond to a change in their thermal environment but this depends on the length of time that the mussels have been acclimated. Furthermore, the change in the two functional responses measured (biodeposition rate and byssus thread production) differed when subject to increased temperature. In the short-term experiment, *M. modiolus* show a shock response to an increase in just 2°C and reduce their biodeposition rate (and therefore presumably their feeding rate). However, when left to acclimate for two months (Experiment 3), biodeposition rate was maintained between 10°C and 16°C, yet beyond this critical limit, *M. modiolus* reduced their deposition rate to a minimal level at 19°C. In both long-term experiments, byssus thread production was lower at higher temperatures (18°C maximum in the Experiment 2 and 19°C in Experiment 3).

Approximate natural summer food concentrations for the *M. modiolus* from Port Appin were achieved during Experiment 3 and the resulting biodeposition rate was 5.49mg mussel^{-1} day^{-1} on average. This is lower than reported by Navarro and Thompson (1997) for *M. modiolus* during a spring bloom (up to 40mg mussel^{-1} day^{-1}) but within those measured outwith the spring bloom (4-8mg day^{-1} mussel^{-1}). The main difference between the two studies is that Navarro and Thompson (1997) used a flow through system with natural seawater whereas the present study used artificial shellfish food. The advantage of using artificial food is that food concentrations can be monitored and modified easily. Food became limited in Experiment 2, therefore biodeposition measurements were not considered to be representative of those experienced by *M. modiolus* in the summer months. It is expected that low food concentrations in the VoRTs during this experiment was a result of the algae settling out in the stock tank.

In Experiment 3 a biphasic biodeposition response was observed. Bayne et al. (1976) suggest that at extremely high temperatures, the high mechanical cost of feeding is greater than the energetic gain; therefore a pause in feeding activity is observed, in order to conserve energetic resources. Historically, when investigating the feeding response of mussels, authors often report a linear increase with temperature (e.g. Walne

1972, Lauringson et al. 2007, Inoue and Yamamuro 2000). However, when exploring beyond the natural thermal envelope experienced by a species, it is common for controlled experiments to show a biphasic response (Schulte 1975, Anestis et al. 2010, Bayne et al. 2012), with an initial increase in feeding rate to an optimal level as metabolic processes increase, then a decline in function at higher temperatures as hypothesised by Willmer et al. (2005).

Thermal tolerance studies often measure mortality of bivalves as a response to temperature (Urban 1994, Rajagopal et al. 2005). However, with rising concerns that climate change may hinder the ability for ecosystems to provide ecosystem services to society (Gosling 2013), it is important to understand the functional response of an organism to changing environmental conditions, especially for those which have a disproportionate effect on the surrounding community, such as ecosystem engineers.

In the present study, when testing a range of thermal conditions which in part, exceed temperatures experienced by *M. modiolus* reefs, a biphasic feeding response is noted, with maximal biodeposition rates at 16°C. However, byssus thread production was more greatly impaired, and displayed a negative response to temperature within the same thermal range. This suggests that when stressed, mussels demonstrate a trade-off between physiological functions, with byssus production being a lower priority than feeding or gonad development for example, as shown by Carrington (2002). The results presented here are consistent with those reported in the literature. For example, Archambault et al. (2013) report an 18-35% decrease in byssus thread production with increasing temperature in freshwater mussels. On the other hand, Garner and Litvaitis (2013) found that *M. edulis* produce more byssus threads in the summer compared to the winter, although this could be due to a number of biotic and abiotic factors, e.g. food availability (Moeser and Carrington 2006).

M. modiolus are a subtidal species, often found in high flow conditions and can occur in dense aggregations (Holt et al. 1998), which build up over time as raised structures on the seabed and provide a habitat for a number of commercially important species (see chapter 2 and 3). Therefore, the formation of byssus threads is a crucial process for binding these mussels together and creating a reef structure. *M. modiolus* are a cold adapted species (Lesser and Kruse 2004) and occur as individuals, from the Arctic to as far south as the Bay of Biscay (Hayward and Ryland 2006, Rees 2009). However, the

reef formations are more limited in distribution and the southernmost reef known is in the Irish Sea where the temperatures reach 16°C each summer and a minimum of just over 6°C in the winter (see appendix D2). This provides some environmental context to the results in the present study, as the production of byssus threads by *M. modiolus* decreased above 16°C but also highlights the importance of understanding the thermal envelope experienced by shellfish species in the wild.

Widdows and Bayne (1971) found that during warm acclimation in *M. edulis,* blood sugar level rises, implying that they start to utilize their energy stores when subject to high temperatures. During Experiment 2, food was at a low concentration and it was observed that byssus thread production was limited at higher temperatures. However, a similar decline in byssus thread production with increasing seawater temperature was observed during Experiment 3, where food concentrations were assumed not to be limited. Byssus thread production may become limited when *M. modiolus* are subject to stressful conditions in order for other biological functions to be maintained. Future experiments that investigate food limitation and temperature as factors would help to understand the utilisation of energy for byssus thread production under stressful conditions and when energy stores are low.

Condition Index (CI) can used to determine the health of shellfish, especially in aquaculture where high flesh : shell ratios are required for the final product (Okumus and Stirling 1998, Gabbott and Walker 1971). In the present study, the condition of *M. modiolus* used in the experiments did not decrease significantly, indicating that food was not limiting.

Many studies show a relationship between mussel condition and season (Blanton et al. 1987, Brown and Hartwick 1988) however, the interaction between changing food concentrations and seawater temperature on the mussel's condition cannot be separated. In the present study all treatments were supplied with the same food concentrations and the only difference in treatments was the temperature. The condition of *M. modiolus* followed a similar pattern to biodeposition rate in response to a change in temperature in Experiment 3 which could indicate that as temperature increases, *M. modiolus* feed more and therefore their condition improves, then past their thermal limit, feeding ceases and the mussels resort to using up energy stores. Hickman et al. (1991) found that abiotic factors (including temperature and salinity) are the most important factors

that determine the condition of *Perna canaliculus* except at low food levels when food availability becomes the main factor.

Condition index is also closely related to gonad development due to the large size of the gonad relative to the total mussel flesh, for example, Bayne et al. (2012) found that when gonads are fully developed, the CI is high and the thermal tolerance is low. Furthermore, Mladineo et al. (2007) found that *M. barbatus* gonad development correlates with ambient temperature. Few studies have fully explained the reproductive cycle of *M. modiolus* and those that have, appear to be inconclusive. Brown (1984) describes the reproductive cycle of *M. modiolus* in different locations and found that for *M. modiolus* from Sweden, gonad development occurs throughout the winter, with ripe mussels spawning in July and August when temperatures are highest. However, *M. modiolus* from Northern Ireland display a slow, continuous release of gametes throughout the year with no defined spawning period (Brown 1984).

Thermal shock can also induce spawning in bivalves (Vélez et al. 1990), therefore, the low CI found in the 10°C and 19°C *M. modiolus* treatments may be due to the mussels spawning when first introduced into their acclimation tanks, although no evidence of spawning was noted at the time. The most pronounced reduction in CI was in the male *M. modiolus* held at 10°C, so perhaps male *M. modiolus* are more sensitive to a change in temperature than females. Mladineo et al. (2007) report an asynchrony of gonad development between male and female *Modiolus barbaratus* and suggest that this is related to the fact that the cost of gametogenesis is lower in males.

The difference in CI reported here for male and female *M. modiolus* could also be linked to the difference in biodeposition rates at different temperatures as mussels are known to utilise the food available in summer months for gonad development (Mladineo et al. 2007). Baghurst and Mitchell (2002) found higher growth rates in female oysters compared to males and suggest that females are able to utilize food more efficiently. Indeed, Tran et al. (2008) found oxygen consumption in male oysters to be twice that of females and attribute this to different energetic requirements for growth as males harbour a greater proportion of protein, which is more energetically demanding to synthesise.

In summary, long-term exposure to high temperatures does affect important functional behaviours that are normally carried out by *M. modiolus* in natural conditions (e.g. biodeposition in chapter 4) and it seems that this has implications for the mussel's condition. However, the exact mechanism driving the changes in *M. modiolus* condition are not clear and would require further investigation into the reproductive cycle of *M. modiolus* in response to temperature, whilst incorporating other pressures such as food limitation.

As mentioned in chapter 1, *M. modiolus* are protected in the UK under the EC Habitats Directive and in Nature Conservation MPAs under the Marine (Scotland) Act 2010, but in both cases it is the reef feature that is protected rather than the individual species. In light of the results presented here, predicted warming may limit the formation of *M. modiolus* reefs and physical impact on existing reefs would hinder reef recovery through byssus attachment in southern populations. Based on the IPCC (2014) best-case scenario of a 1.8°C increase in ocean surface temperature, the Pen Llŷn *M. modiolus* reef would be above the 16°C threshold for the production of byssus for almost a third of the year (32%). However, the worst-case scenario of a 4°C increase would escalate this proportion to 51%. Though, this projection must be used with care as the IPCC predictions are based on sea surface temperatures and *M. modiolus* will experience slightly different seawater temperatures at ~30m below chart datum, depending on the level of stratification.

A reduction in the production of byssus threads by *M. modiolus* reef populations may increase habitat fragmentation, which will reduce connectivity of biogenic reef habitats protected within MPAs. Therefore, in order to be effective, Marine Spatial Planning should take into account the modification of ecological processes and the poleward redistribution of biodiversity hotspots in response to climate change (Gormley et al. 2015, Burrows et al. 2011). In addition, management decisions for MPAs should consider the loss of ecological function and reduced resilience of communities that are subject to multiple pressures.

Chapter 6. General Discussion

The purpose of this thesis was to investigate and quantify key ecosystem services provided by *Modiolus modiolus* reefs and to investigate the impact of increased seawater temperature on *M. modiolus* function and associated services. The research presented here (chapters 2 and 3) has demonstrated that *M. modiolus* reefs provide a habitat for commercially important megafaunal species, in particular, *Buccinum undatum* and *Aequipecten opercularis.* Mobile fauna were also attracted into experimental chambers containing *M. modiolus* used in chapter 4 which, although not designed to trap animals, were found to contain significantly more crustaceans compared to the control (empty) chambers. Similar chambers have also been used by Kellogg et al. (2011) to trap megafauna and measure nutrient sequestration on an oyster (*Crassostrea virginica*) reef. The results from chapter 2 are consistent with experiments on maerl beds, whereby the habitats do not only support commercially important species but show a greater abundance of other large invertebrates such as *Echinus esculentus* and *Asterias rubens* (Kamenos et al. 2004b).

Modiolus modiolus Reefs as Essential Fish Habitats

The experiments presented in chapters 2 and 3 are the first to directly measure habitat associations on *M. modiolus* reefs with experimental controls, however, the results are in line with observations from previous studies on *M. modiolus* reefs. For example, *B. undatum* and *A. opercularis* were also highlighted as being key species contributing to the difference in the community structure of *M. modiolus* reefs in Strangford Lough, with both species being twice as abundance before a period of trawling activity than after (Strain et al. 2012). When considering all the evidence together (from chapters 2 and 3 and research in Strangford Lough), it becomes clear that there is a strong association between *M. modiolus* reefs and both *B. undatum* and *A. opercularis*. Strain et al. (2012) suggest that this possible association has resulted in *M. modiolus* reefs being targeted by fishing vessels and ultimately, leading to the demise of this biogenic habitat. It is likely that this has been the case for *M. modiolus* reefs throughout Europe and this illustrates the disadvantages of highly productive habitats in their ability to provide provisioning services to society, as it is this very role that can make the habitats vulnerable to damage from the exploitation of commercially important species.

The stable isotope data (chapter 2) show that *M. modiolus* feed at a higher trophic level than *A. opercularis* and there was no overlap in the isotopic signatures of the two species despite the fact that both species acquire food by filter feeding. This reveals further niches within the reef, beyond the physical spaces. *M. modiolus* and *A. opercularis* may have different feeding strategies due to their different social behaviours, i.e. *M. modiolus* tend to aggregate whereas *A. opercularis* are solitary. Widdows et al. (2009) demonstrate that where there is a large collection of individuals such as in mussel beds, resuspension of sediments is more likely to occur. One could therefore hypothesise that *M. modiolus* may be more adapted to feed on resuspended material (including bacteria and animal remains etc.) to make the most of any available food, whereas *A. opercularis* are not adapted to this situation.

The selection of particles by filter feeders may depend on whether the bivalve lives infaunally or epifaunally as shown by Hawkins et al. (1998) and this could manifest itself as a different isotopic signature of the adductor muscle. On the other hand the two species may simply selectively feed on different planktonic assemblages based on the size, nutritional quality or chemical nature of the particles (Ward et al. 1997, Ward and Shumway 2004).

The natural diet of bivalve molluscs is not well defined in the literature; it is generally assumed that mussels are herbivorous due to their ability to clear high densities of phytoplankton from the water column and from evidence of diatoms in stomach contents (Lopes-Lima et al. 2014). However, Lehane and Davenport (2002) found a high proportion of zooplankton in the diet of *A. opercularis* and *Mytilus edulis.* Additionally, Biandolino et al. (2008) found that phytoplankton comprise only a minor portion of the diet of *Mytilus galloprovincialis*. The present results add weight to the view that bivalves are not simple on-off mechanisms and may be niche partitioned in subtle ways.

Sediment Sequestration by Modiolus modiolus Reefs

Chapter 4 highlights the importance of *M. modiolus* reefs for bentho-pleagic coupling, whereby *M. modiolus* enhance the downward flux of material from the water column into the reef where it becomes locked into the seabed. In this experiment the Total Particulate Matter was measured but the chemical makeup of this sediment was not analysed as this was not the initial purpose of the experiment. However, the sediment

samples collected on a *M. modiolus* reef for stable isotope analysis were analysed for carbon content (organic and inorganic) once sieved on a 63µm sieve to remove shell fragments. The average proportion of carbon in the sediment samples collected was 10.87% by dry weight; therefore, based on the enhanced deposition rates calculated in this chapter and extrapolated for a year, *M. modiolus* reefs have the potential to sequest an estimated 169g C m^{-2} yr^{-1} (see appendix E1).

Burrows et al. (2014) estimate that *M. modiolus* reefs in Scotland sequest 40 g C m^{-2} yr^{-1}, however, this is purely based on the proportion of carbon in the shell material (12%). Molluscs convert CO_2 into calcium carbonate during exoskeleton formation and it has been suggested that this process could play a key role in CO_2 capture technology (Lee et al. 2010). However, a greater understanding of the processes that occur once the mussels die is required, including the rate at which bivalve shell dissolves back into the water column. According to Lee et al. (2010) calcium carbonate is a stable mineral in most environments, and CO_2 can be stored in this form for periods of time measured in millennia. Therefore, the dissolution process may be insignificant on shellfish reefs, especially on *M. modiolus* reefs where the shell material is largely buried within the three-dimensional structure and not directly exposed to the water column.

The estimation of carbon sequestration given above is much higher than Burrows et al. (2014) as it takes into account the enhanced draw down of material by *M. modiolus* through active and passive processes, which has not been measured before in the wild and was therefore not considered in the calculations by Burrows et al. (2014). However, 169g C m^{-2} yr^{-1} may be an overestimation of carbon sequestration through biodeposition as the *in situ* sedimentation experiment was carried out in July, which is not representative of the annual feeding regime and seasonal changes in environmental conditions. Further experiments into the seasonal variation in deposition rates and an investigation into the contribution of organic and inorganic carbon stored in different layers of the reef would be required to make a more accurate estimation of carbon storage in *M. modiolus* reefs.

Ecosystem Services and Marine Spatial Planning

Ecosystem services research is rarely taken into consideration in marine spatial planning (MSP) (Bohnke-Henrichs et al. 2013) or the management of MPAs (Crowder and Norse 2008). However, it is important to consider how activities might have an

impact on the function of protected features when considering the size and shape of an MPA or the restriction of certain activities. For example, the Noss Head MPA was designated for the horse mussel reef feature and mobile fishing is to be prohibited here due to the sensitivity of horse mussels to physical impact and sedimentation which can result in significant mortalities (Marine Scotland 2014, SNH 2013). However, these impacts may also affect the function of *M. modiolus* (e.g. filter feeding) and therefore have a knock-on effect on the ecosystem services provided by the reef, ultimately having a negative effect on society.

Industries that make use of natural resources can be integrated into the management of protected areas through the 'trade' of ecosystem services, for example, land owners can be paid to manage their land in ways which achieve conservation objectives. If ecosystem services are not valued or even considered in management decisions, resource users generally do not take into account the degradation of services in the way that they utilise resources (Corbera et al. 2007). Identifying possible trade-offs between different ecosystem goods and services could facilitate decision analysis and optimisation of the marine area (Tuda et al. 2014). However, our understanding of the relationship between ecological functions and the delivery of services (and therefore benefits to society) is limited, and the present study is a rare example.

The Pen Llŷn case study described in chapter 3 provides an example of a reef ecosystem that is providing a service but the interaction between the resource and users must be considered further. The *M. modiolus* reefs support a considerable population of *B. undatum*, which is important for the livelihoods of local fishers and spatial management excludes mobile fishing gear from the reefs to protect the reefs. There is limited evidence of the impact of static fishing gear on the seabed (Eno et al. 2001), however under strong tidal conditions, a string of pots can be dragged for approximately 10 minutes on the Pen Llŷn (F. Kent, pers. obs.) and intense pot fishing is likely to cause damage to the fragile reef epifauna.

The two closed areas shown in Figure 12 (chapter 3) demonstrate quite different management approaches; both are closed to mobile fishing gear, yet the northern closed area (b) more tightly fits the reef area while closed area (a) provides a much larger buffer around the reef. During the scallop dredging season when pots are confined to the closed areas (due to gear conflict), fishing effort is probably spread over the reef *and*

adjacent areas within the southern closed area (a), whereas in the northern closed area (b) fishing effort is probably disproportionately *on* the reef.

Higher pot fishing activity on the northern reef (area b; Figure 12) suggests that there is a greater risk of not achieving the conservation objectives for this site and deterioration of the reef could result in lower catch rates for the whelk fishery, if pot-dragging is a significant impact. However, a thorough investigation into the long-term impact of static fishing gear on *M. modiolus* habitats and the small-scale distribution of fishing effort in the area would be beneficial, and has not yet been considered. Continued engagement with fishers may also result in improved fishing practices if the current methods are found to be harmful. This approach can also be used to develop management advice at a local scale but also to inform policy on the interactions between sectors which can arise as a consequence of enforcement on a national scale (e.g. gear conflict; Mangi at al. 2011).

The Loss of Biogenic Habitats

Historical evidence from the North East Atlantic suggests that large areas of shellfish habitats have been lost over the past 200 years. Olsen (1883) reported a native oyster bed covering approximately 48,000km^2 in the North Sea and several others. Similarly, the Firth of Forth had a 20 mile long shellfish reef (Thurstan et al. 2013) and the 'Oystermouth' fishery in South Wales supported 200 vessels and up to 400 men in the mid-1800s (WWF 2012). *M. modiolus* reefs have not been targeted by fisheries in the same way as oyster reefs but have probably been incidentally damaged by mobile fishing gear (Cook et al. 2013) by vessels targeting associated species (chapter 2).

The wide scale loss of shellfish habitats in the coastal waters of the NE Atlantic is likely to have resulted in a loss of ecosystem functions and services (e.g. a loss of habitat for commercially important species). It is likely that the remnant shellfish reefs that exist today provide only a fraction of the functional benefits that they probably did in the past. However, research from the USA (e.g. Chesapeake Bay) has shown that restoration of reefs formed by the American oyster (*Crassostrea virginica*) can enhance ecosystem services (Kellogg et al. 2011, Grabowski and Peterson 2007, Peterson et al. 2003). Experimental restoration of *M. modiolus* habitat in Strangford Lough commenced in 2008 through the deployment of cultch material seeded with live *M. modiolus* (Farinas-Franco and Roberts 2014, Roberts et al. 2011). However, the

ecosystem benefits provided by this work are unlikely to take effect immediately, given the timescales involved in *M. modiolus* reef formation.

The Impact of Temperature on Ecosystem Services

The evidence given in this thesis shows the importance of *M. modiolus* reefs in regard to the ecosystem services that they provide to society. The ecological functions and corresponding ecosystem services examined in this study are summarised in Figure 38. It has also been demonstrated that when subject to a stressor (i.e. increased temperature in this case), the ability for *M. modiolus* to function and therefore carry out ecosystem services is disrupted. Short term impacts (i.e. extreme climatic events, such as heat waves) can cause the filtration behaviour in *M. modiolus* to shut down and it has been shown that heat wave events can structure marine populations (e.g. kelp; Smale and Wernberg 2013). The response of ecosystems to extreme weather episodes depends on the frequency and intensity of the events; many species have shown a shift in their range over geological timescales, while others adapt over time (Parmesan et al. 2000).

Until recently, research on the ecosystem effects of climate change has focused on long-term trends, for example, Hawkins et al. (2009) describe the poleward movement of intertidal species over the past 50-100 years. However, the importance of 'event-focused' research is now being recognised (Jentsch et al. 2007). Event-focused research investigates individual weather events that are statistically extreme and short in duration. Also, the timing of such events can be more important than the scale of the event itself. For example, the northern limit of deciduous trees is driven by minimum winter temperatures in the northern hemisphere, yet the timing of an extreme frost event is more important than the temperature itself (Jentsch et al. 2007).

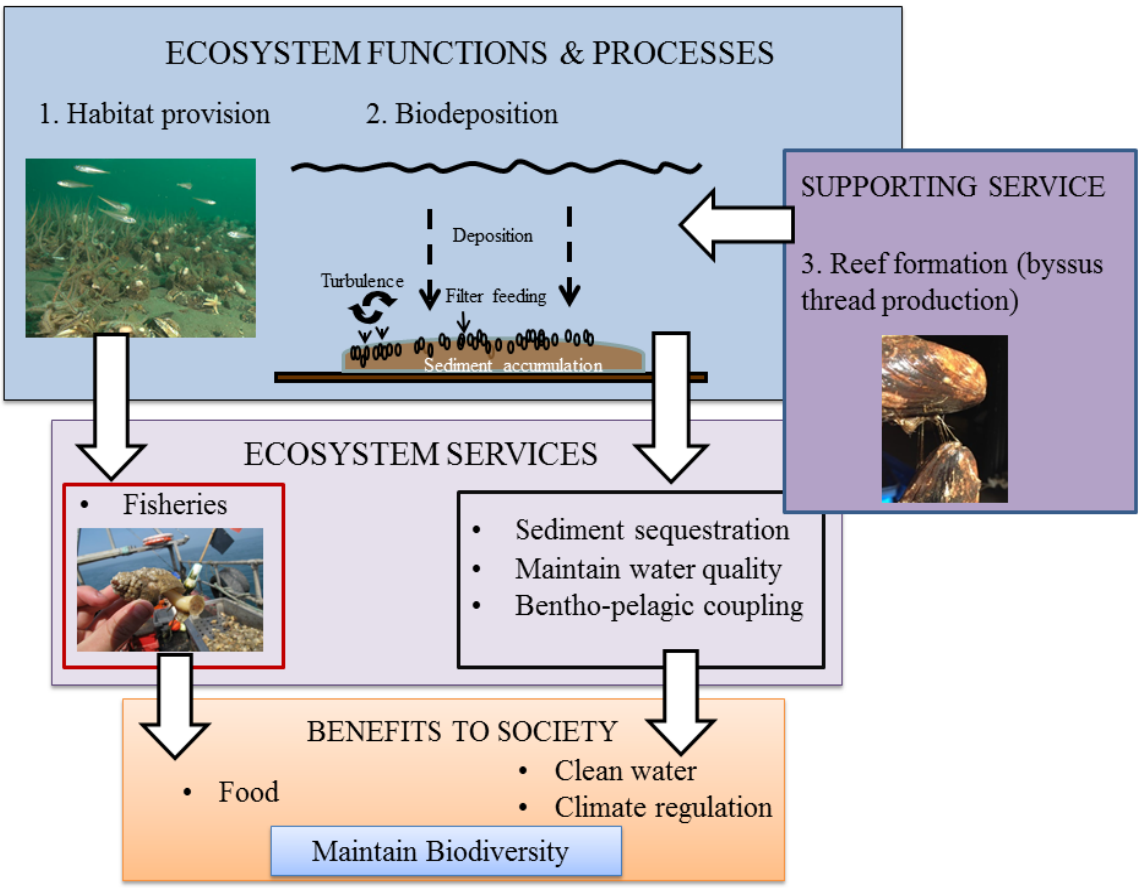

Figure 38. A framework of the ecosystem services provided by *Modiolus modiolus* reefs and associated processes and benefits. Services are split into provisional services (red box), regulating services (black box) and supporting services (purple box).

The long-term outlook for *M. modiolus* reefs is a concern given their widespread decline over the past 200 years. This is largely attributable to destructive fishing techniques (Thurstan et al. 2013, Cook et al. 2013, Strain et al. 2012), but the predicted loss of suitable conditions for *M. modiolus* reefs with rising seawater temperatures in southern locations is also a concern (Gormley et al. 2013). When exposed to increased seawater temperature after a long acclimation period (chapter 5), the most striking response seen in *M. modiolus* was a reduction in byssus thread production. Attachment by byssus threads is important for reef formation but also for the survival of *M. modiolus* in early life stages. It has been suggested that the matrix created by *M. modiolus* byssus threads within clumps provide a refuge for *M. modiolus* spat (Fariñas-Franco et al. 2013).

According to Lane et al. (1985), young post-larval mussels produce 'drifting threads', which are longer than the 'attachment threads' produced by adults and assist with dispersal by acting like a sail in the water column. Furthermore, young mussels are able to select a surface to attach to based on factors such as the presence of predators (Cheung et al. 2004), substrate colour and other environmental factors (Kobak 2001). Future studies would benefit from an investigation into the effect of temperature on byssus thread production in juvenile *M. modiolus*, as this could have significant implications for recruitment and recovery of *M. modiolus* reefs following a disturbance.

With predicted warming, *M. modiolus* reefs may persist in the short-term but will not be able to function to their full extent. In addition, if supporting services are removed, this could have serious implications for other services. For example, reef development is partly dependent on clump formation by byssus thread attachment (Erlandsson et al. 2011), however, if *M. modiolus* are unable to produce byssus at elevated temperatures, this feature will be compromised. Reef formation is important for supporting other services including sediment accumulation and habitat provision (Figure 38). It is expected that individual scattered *M. modiolus* would not accumulate sediment to the same extent as those in dense aggregations because the sediment and shell fragments would be washed away more easily, especially under high flow conditions. This would result in a loss of those services connected to reef formation, such as sediment stabilisation and carbon sequestration. The role of *M. modiolus* reefs as an EFH may also be jeopardised without reef formation because there would be less food available

for associated species such as *B. undatum* to forage for and fewer niches to protect juveniles from predators.

Conclusion

M. modiolus reefs are subject to multiple pressures and MPAs already exist to conserve this habitat as a biogenic reef feature. However most MPAs are multi-use areas, which only restrict specific activities (e.g. mobile fishing only as seen in chapter 3) and the damage caused by permitted activities such as pot fishing, is often unknown. A key limitation of MPAs is that they cannot protect against large scale, unpredictable pressures such as extreme weather events or chemical pollution. Ecosystem resilience relies on healthy populations of key functional species and high diversity (McLeod et al. 2008, Hughes et al. 2005). For habitats subject to multiple pressures, resilience can be increased by removing manageable anthropogenic impacts on a local scale (Ruckelshaus et al. 2008). For example, the removal of fishing pressure in fully protected marine reserves can enhance fish stocks, restore the natural age structure of fish populations and maintain genetic diversity, therefore making the system more resilient to changes in the environment and unpredictable events (Roberts et al. 2005).

The results presented here show that fragile biogenic structures, such as those created by *M. modiolus* are functionally important and therefore should be considered a high priority for rigorous management measures in MPAs. Research into ecosystem services can further our understanding of the ecology of benthic habitats and support marine policy decisions. Further research into the impact of static fishing gear (e.g. whelk pots) and environmental parameters, such as salinity and hypoxia, would build upon our current knowledge of biogenic reef ecology and assist with the design and management of MPAs. In order to develop resistance to unpredictable climatic events and changing environmental conditions, all manageable pressures should be removed for *M. modiolus* reef features. This would increase the chance of habitat recovery if subject to an unpredictable disturbance event.

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Appendices

Chapter 2

Appendix A1. UVC megafauna identification training sites surveyed in May 2012 during a pilot study.

Date	Site	Latitude		Longitude		Diver	Depth	Habitat
08/05/2012	Toyness West	58	54.914	3	8.689	FK	25	Muddy Sand
09/05/2012	East Waulk Mill Bay	58	56.101	3	3.225	FK	25	Muddy Sand
09/05/2012	Holm of Houton	58	54.754	3	10.353	FK	23	Muddy Sand
10/05/2012	South Flotta	58	48.749	3	6.529	FK	24	Rock
06/05/2012	Rysa Little 1	58	52.131	3	11.729	FK	22.4	Modiolus
06/05/2012	Rysa Little 2	58	52.131	3	11.729	HM	22.4	Modiolus
11/05/2012	Karlsrhue 1	58	53.357	3	11.394	FK	26	Modiolus
11/05/2012	Karlsrhue 2	58	53.357	3	11.394	BS	26	Modiolus
06/05/2012	Cava Island 1	58	53.162	3	10.311	FK	12.6	Sand algae
06/05/2012	Cava Island 2	58	53.162	3	10.311	HM	12.6	Sand algae anemones
07/05/2012	Gutter sound	58	51.581	3	11.034	FK	20	Modiolus
07/05/2012	West Cava	58	52.718	3	11.458	FK	24.6	Modiolus
08/05/2012	East Fara	58	50.966	3	11.041	FK	16	Modiolus

Appendix A2. UVC megafauna data obtained during training session in May 2012 in Scapa Flow, Orkney.

Site	***E. esculentus***	***P. maximus***	***B. undatum***	***A. opercularis***	***P. pictus***	***G. flavescens***	***P. gunnellus***	***L. lampretaeformis***	***C. maenas***
Toyness West	0	0	0	1	3	0	0	0	0
East Waulk Mill Bay	0	0	0	0	11	0	1	0	0
Holm of Houton	1	1	0	0	6	0	0	0	0
South Flotta	0	4	0	0	1	8	0	0	0
Rysa Little 1	7	0	2	31	0	0	0	0	0
Rysa Little 2	13	1	1	48	0	0	0	0	0
Karlsrhue 1	17	3	3	23	0	0	1	0	0
Karlsrhue 2	4	0	4	7	0	0	0	0	0
Cava 1	1	1	0	0	0	0	0	0	0
Cava 2	3	0	0	0	0	0	0	0	0
Gutter sound	0	1	2	0	1	10	0	0	0
West Cava	5	0	0	8	0	0	0	0	0
East Fara	2	1	0	3	2	22	1	1	3

Appendix A3. Seabed habitat type percentage cover derived from photoquadrats in order to define habitats as either *M. modiolus* reef, cobble or sand.

Date	Site Location	Site Code	Latitude (D.MM)		Longitude (D.MM)		Depth (m)	Modiolus Density (no. per m2)	Habitat method	Habitat
05/09/2012	Burraness	Shet_1	60	37.99	0	59.25	20	0	Quadrats	Cobbles
07/09/2012	Knab deep	Shet_2	60	8.737	1	7.925	24	0	Quadrats	Cobbles
07/09/2012	Knab shallow	Shet_3	60	8.774	1	8.226	17	0	Quadrats	Cobbles
12/05/2013	S7 Shapinsay	ORK_1	59	0.991	2	43.394	25	0	Quadrats and PSA	Cobbles
14/05/2013	South Flotta	ORK_2	58	48.749	3	6.529	24	0	Quadrats and PSA	Cobbles
17/05/2013	South Flotta Bay	ORK_3	58	48.773	3	6.892	24	0	Quadrats and PSA	Cobbles
17/05/2013	South Flotta Bay	ORK_4	58	48.757	3	7.175	25	0	Quadrats and PSA	Cobbles
02/09/2012	Outer Basta Voe	SHET_4	60	37.896	0	59.665	20	16	Quadrats	Modiolus
03/09/2012	Uyea Sound	SHET_5	60	40.022	0	56.641	22	24	Quadrats	Modiolus
05/09/2012	Hascosay Sound	SHET_6	60	37.0864	1	0.454	17	82	Quadrats	Modiolus
06/09/2012	Calbackness	SHET_7	60	29.32	1	16	22	33	Quadrats and PSA	Modiolus
13/05/2013	Karlsrhue New1	ORK_5	58	53.39	3	11.122	19	28	Quadrats and PSA	Modiolus
14/05/2013	Karlsrhue New2	ORK_6	58	53.391	3	11.182	20	23	Quadrats and PSA	Modiolus
16/05/2013	Karlsrhue New3	ORK_7	58	53.362	3	11.145	21	31	Quadrats and PSA	Modiolus
16/05/2013	Karlsrhue New4	ORK_8	58	53.332	3	11.116	20	23	Quadrats	Modiolus
05/09/2012	Uyea Sound West	SHET_8	60	40.538	0	55.418	15	0	Quadrats	Sand
05/09/2012	Uyea Sound East	SHET_9	60	40.3017	0	51.9527	22	0	Quadrats	Sand
06/09/2012	Calbackness Control	SHET_10	60	29.507	1	15.738	20	0	Quadrats	Sand
06/09/2012	Calbackness Control	SHET_11	60	29.623	1	14.532	24	0	Quadrats	Sand
12/05/2013	D9 Deer Sound	ORK_13	58	58.278	2	45.938	17	0	Quadrats and PSA	Sand
12/05/2013	D14 Deer Sound	ORK_14	58	58.575	2	47.075	22	0	Quadrats and PSA	Sand
12/05/2013	D13 Deer Sound	ORK_15	58	58.566	2	46.305	22	0	Quadrats and PSA	Sand
12/05/2013	NEW Deer Sound	ORK_16	58	58.28	2	46.496	17	0	Quadrats and PSA	Sand

Appendix A4. Drop Down Video megafauna survey sites (Pen Llŷn, North Wales) and metadata.

Site Code	Start Position		End Position		Depth	Habitat	Distance	Speed meters per minute	Complexity
NW_7	52.93752	-4.61025	52.9381	-4.6095	22	Sand/Gravel	82	16	2
NW_17	52.97103	-4.62007	52.9705	-4.62083	31	Sand/Gravel	79	16	2
NW_2	52.97108	-4.61658	52.97043	-4.61693	31	Sand/Gravel	<50	9	2
NW_4	52.96542	-4.65245	52.96643	-4.65233	36	Sand/Gravel	113	23	2
NW_3	52.9979	-4.61368	52.99847	-4.615	32	Sand/Gravel	109	22	2
NW_1	52.99903	-4.62347	52.99985	-4.52368	32	Sand/Gravel	90	16	2
NW_2	52.99657	-4.56125	52.99662	-4.56317	20	Sand/Gravel	129	26	2
NW_15	52.94075	-4.58603	56.45	-4.01568	17	Sand/Gravel	92	16	2
NW_C2	52.93867	-4.6416	52.93828	-4.64235	32	Modiolus	66	12	3
NW_03	52.94072	-4.64337	52.94165	-4.64302	33	Modiolus	47	10	3
NW_10	52.94358	-4.65247	52.94423	-4.65132	33	Modiolus	106	20	3
NW_22	52.94627	-4.64535	52.94677	-4.6462	32	Modiolus	80	16	3
NW_1	53.00475	-4.55592	53.00483	-4.55682	21	Modiolus	61	11	3
NW_1b	53.00475	-4.55592	53.00483	-4.55682	21	Modiolus	<50	9	3
NW_26	52.94233	-4.63627	52.9421	-4.63685	30	Modiolus	47	9	3
NW_A4	52.8763	-4.69333	52.87593	-4.69377	17	Boulders	50	10	5
NW_5	52.86798	-4.70282	52.86867	-4.70257	20	Boulders	78	13	5
NW_A10	52.87072	-4.69732	52.87118	-4.88	17	Boulders	80	23	5
NW_A7	52.87227	-4.69872	52.87285	-4.69757	20	Boulders	101	21	5
NW_02	52.87298	-4.70157	52.87403	-4.7008	25	Boulders	128	26	5
NW_19	52.87933	-4.70072	52.88003	-4.70125	24	Boulders	86	17	5
NW_13	52.88352	-4.68872	52.883	-4.68983	17	Boulders	<50	9	5
NW_7	52.87672	-4.70078	52.555	-4.0146	23	Boulders	140	23	5

Appendix A5. Seabed habitat type percentage cover derived from photoquadrats in order to define the habitats as either *M. modiolus* reef, cobble or sand.

Site	% Live *Modiolus*	Boulders	Cobbles	Pebbles	Broken Shell	Fine Sand	Coarse sand	Mud	Sediment type
Outer Basta Voe	15	0	0	10	10	65	0	0	Modiolus
Outer Basta Voe	10	0	0	10	10	70	0	0	Modiolus
Outer Basta Voe	40	0	0	5	5	50	0	0	Modiolus
Outer Basta Voe	40	0	0	5	5	50	0	0	Modiolus
Outer Basta Voe	35	0	0	5	5	55	0	0	Modiolus
Outer Basta Voe	5	0	0	10	10	75	0	0	Modiolus
Burraness	0	0	0	20	10	0	70	0	Cobbles
Burraness	0	0	0	30	20	0	50	0	Cobbles
Burraness	0	0	0	50	30	0	20	0	Cobbles
Burraness	0	0	0	10	10	0	80	0	Cobbles
Hascosay Sound	80	0	0	0	10	0	0	10	Modiolus
Hascosay Sound	70	0	0	0	0	10	0	20	Modiolus
Hascosay Sound	80	0	0	0	0	10	0	10	Modiolus
Hascosay Sound	80	0	0	0	0	10	0	10	Modiolus
Hascosay Sound	80	0	0	0	0	10	0	10	Modiolus
Uyea Sound East	0	0	0	0	20	0	80	0	Sand
Uyea Sound East	0	0	0	0	20	0	80	0	Sand
Uyea Sound East	0	0	0	0	10	0	90	0	Sand

Uyea Sound East	0	0	0	0	0	0	100	0	Sand
Uyea Sound East	0	0	0	0	5	0	95	0	Sand
Uyea Sound West	0	0	0	0	10	0	90	0	Sand
Uyea Sound West	0	0	0	0	0	0	100	0	Sand
Uyea Sound West	0	0	0	0	0	0	100	0	Sand
Uyea Sound West	0	0	0	0	5	0	95	0	Sand
Uyea Sound West	0	0	0	0	5	0	95	0	Sand
Uyea Sound West	0	0	0	0	0	0	100	0	Sand
Calbackness control BS	0	0	0	0	0	0	100	0	Sand
Calbackness control BS	0	0	0	0	5	0	95	0	Sand
Calbackness control BS	0	0	0	0	10	0	90	0	Sand
Calbackness control BS	0	0	0	0	0	0	100	0	Sand
Calbackness	0	0	0	0	20	0	80	0	Sand

control FK									
Calbackness control FK	0	0	0	0	25	0	75	0	Sand
Calbackness control FK	0	0	0	0	35	0	65	0	Sand
Calbackness control FK	0	0	0	0	40	0	60	0	Sand
Calbackness control FK	0	0	0	0	30	0	70	0	Sand
Calbackness control FK	0	0	0	0	50	0	50	0	Sand
Calbackness control FK	0	0	0	0	40	0	60	0	Sand
Calbackness Modiolus	20	0	0	0	0	10	0	70	Modiolus
Calbackness Modiolus	20	0	0	0	0	10	0	70	Modiolus
Calbackness Modiolus	25	0	0	0	0	10	0	65	Modiolus
Calbackness Modiolus	30	0	0	0	0	10	0	60	Modiolus
Calbackness Modiolus	40	0	0	0	0	10	0	50	Modiolus

Calbackness Modiolus	30	0	0	0	0	10	0	60	Modiolus
Knab deep	0	0	0	20	40	0	0	40	Cobbles
Knab deep	0	0	0	30	60	0	0	10	Cobbles
Knab deep	0	0	0	30	60	0	0	10	Cobbles
Knab deep	0	0	0	30	50	0	0	20	Cobbles
Knab deep	0	0	0	10	70	0	0	20	Cobbles
Knab deep	3	0	0	10	80	0	0	10	Cobbles
Knab shallow	0	60	0	20	10	10	0	0	Cobbles
Knab shallow	0	70	0	15	5	10	0	0	Cobbles
Knab shallow	0	70	0	15	5	10	0	0	Cobbles
Knab shallow	0	70	0	10	10	10	0	0	Cobbles
Knab shallow	0	40	10	20	20	0	10	0	Cobbles
Knab shallow	3	30	15	30	20	0	5	0	Cobbles
Knab shallow	0	20	10	20	20	30	0	0	Cobbles
D13	0	0	0	0	20	30	50	0	Sand
D13	0	0	0	0	10	50	35	5	Sand
D13	0	0	0	0	10	40	40	10	Sand
D13	0	0	0	0	5	40	40	15	Sand
New deer sound	0	0	0	0	10	40	30	20	Sand
New deer sound	0	0	0	0	10	40	30	20	Sand
New deer sound	0	0	0	0	50	10	40	0	Sand
New deer sound	0	0	0	0	10	60	10	20	Sand

Karls new 2	30	0	0	0	30	30	0	10	Modiolus
Karls new 2	40	0	0	0	5	50	0	5	Modiolus
Karls new 2	40	0	0	0	5	50	0	5	Modiolus
Karls new 2	60	0	0	0	5	30	0	5	Modiolus
South Flotta	0	30	50	10	5	0	5	0	Cobbles
South Flotta	0	10	50	20	10	5	5	0	Cobbles
South Flotta	0	5	20	50	10	5	10	0	Cobbles
South Flotta	0	5	40	40	10	0	5	0	Cobbles
Karls new 3	50	0	0	0	0	10	0	40	Modiolus
Karls new 3	40	0	0	0	0	10	0	50	Modiolus
Karls new 3	40	0	0	0	0	10	0	50	Modiolus
Karls new 3	40	0	0	0	0	10	0	50	Modiolus
Karls new 4	80	0	0	0	0	10	0	10	Modiolus
Karls new 4	80	0	0	0	0	10	0	10	Modiolus
Karls new 4	90	0	0	0	0	5	0	5	Modiolus
Karls new 4	50	0	0	0	0	10	0	40	Modiolus
South Flotta 71	0	10	30	30	10	0	20	0	Cobbles
South Flotta 71	0	50	30	10	5	0	5	0	Cobbles
South Flotta 71	0	60	20	10	5	0	5	0	Cobbles
South Flotta 71	0	60	20	10	5	0	5	0	Cobbles
South Flotta 71	0	80	10	5	0	0	5	0	Cobbles
D9	0	0	0	0	10	20	60	10	Sand
D9	0	0	0	0	10	20	50	20	Sand

D9	0	0	0	0	10	20	50	20	Sand
D9	0	0	0	0	10	20	50	20	Sand
D9	0	0	0	0	10	20	50	20	Sand
D9	0	0	0	0	10	20	50	20	Sand
S7	0	25	40	5	20	0	10	0	Cobbles
S7	0	80	10	0	5	0	5	0	Cobbles
S7	0	80	10	0	5	0	5	0	Cobbles
S7	0	90	0	0	0	0	10	0	Cobbles
S7	0	90	0	0	0	0	10	0	Cobbles
Karls new 1	0	0	0	0	0	0	0	100	Modiolus
Karls new 1	0	0	0	0	0	0	0	100	Modiolus
Karls new 1	0	0	0	0	0	0	0	100	Modiolus
D14	0	0	0	0	10	10	70	10	Sand
D14	0	0	0	0	5	20	70	5	Sand
D14	0	0	0	0	20	5	70	5	Sand
D14	0	0	0	0	30	10	50	10	Sand
Uyea sound	50	0	0	0	0	50	0	0	Modiolus
Uyea sound	40	0	0	0	0	60	0	0	Modiolus
Uyea sound	30	0	0	0	0	70	0	0	Modiolus
Uyea sound	40	0	0	0	0	60	0	0	Modiolus

Appendix A6. Underwater Visual Census (UVC) key species pairwise comparisons (Kruskal Wallis tests), Bonferroni correction; significance at $p < 0.016$.

Key Species	Habitat comparison	X^2	P value
Buccinum undatum	Reef & Cobble	3.84	0.0500
	Reef & Sand	7.1358	0.0076
	Cobble and Sand	0.686	0.4073
Aequipecten opercularis	Reef & Cobble	11.0112	0.0009
	Cobble & Sand	0.6868	0.4073
	Reef & Sand	12.4272	0.0004
Echinus esculentus	Reef & Cobble	9.422	0.0021
	Cobble & Sand	10.8482	0.0009
	Reef & Sand	12.3077	0.0005

Appendix A7. Drop Down Video (DDV) key species pairwise comparisons (Kruskal Wallis tests), Bonferroni correction; significance at $p < 0.016$.

Key Species	Habitat comparison	X^2	P value
Buccinum undatum	Reef & Cobble	6.55	0.0100
	Reef & Sand	0.0269	0.8690
	Cobble & Sand	6.5502	0.0100
Maja brachydactyla	Reef & Cobble	2.6042	0.1066
	Reef & Sand	2.6042	0.1066
	Cobble & Sand	0	1.0000
Asterias rubens	Reef & Cobble	9.258	0.0023
	Cobble & Sand	0.0509	0.8214
	Reef & Sand	11.618	0.0007

Appendix A8. Species list and Biological Trait Analysis characteristics table

Species	Mobility	Vertical position	Feeding mechanism	Longevity	Trophic level	Body Size
Aequipecten	Slow	Benthic	Filter Feeder	Long	1	Small
Aspitrigla	Slow	Demersal	Predatory	Medium	5	Large
Asterias	Slow	Benthic	Scavenger	Medium	4	Large
Buccinum undatum	Slow	Benthic	Scavenger	Long	3	Small
Callionymus	Fast	Demersal	Predatory	Medium	4	Large
Cancer pagurus	Slow	Benthic	Predatory	V. long	3	Large
Carcinus maenas	Slow	Benthic	Predatory	Medium	3	Small
Clupea	Fast	Demersal	Predatory	V. long	5	Large
Crossaster	Slow	Benthic	Scavenger	Medium	4	Large
Diplecogaster bimaculata	Fast	Demersal	Predatory	Short	4	Small
Scyliorhinus canicula	Fast	Demersal	Predatory	Long	5	Large
Echinus	Slow	Benthic	Scavenger	Medium	2	Small
Eledone	Slow	Benthic	Scavenger	Short	3	Large
Gadoid	Fast	Demersal	Predatory	V. long	5	Large
Gobiusculus flavescens	Fast	Demersal	Predatory	Short	4	Small
Goldsinny Wrasse	Fast	Demersal	Predatory	V. long	5	Large
Hommarus	Slow	Demersal	Predatory	V. long	3	Large
Labrus bergylta	Fast	Demersal	Predatory	V. long	5	Large
Labrus mixtus	Fast	Demersal	Predatory	V. long	5	Large
Limanda limanda	Fast	Demersal	Predatory	V. long	5	Large
Lumpenus lampretaeformis	Fast	Demersal	Predatory	Short	4	Large
Maja	Slow	Benthic	Predatory	Long	4	Large
Myoxocephalus scorpius	Fast	Demersal	Predatory	Medium	4	Large
Necora puba	Slow	Demersal	Predatory	Medium	3	Small
Pecten maximus	Sedentary	Benthic	Filter Feeder	Long	1	Large
Pholis gunnellus	Fast	Demersal	Predatory	Medium	4	Large
Pollachius virens	Fast	Demersal	Predatory	Long	5	Large
Pomatoschistus microps	Fast	Demersal	Predatory	Short	4	Small
Pomatoschistus pictus	Fast	Demersal	Predatory	Short	4	Small
Pomatoschistus spp	Fast	Demersal	Predatory	Short	4	Small
Raja	Fast	Demersal	Predatory	V. long	5	Large
Necora puber	Slow	Demersal	Predatory	V. long	3	Small
Taurulus bubalis	Fast	Demersal	Predatory	Medium	4	Large
Phrynorhombus norvegicus	Fast	Demersal	Predatory	V. long	5	Large
Trisopterus	Fast	Demersal	Predatory	V. long	5	Large

Chapter 3

Appendix B1. Fishing sites off the Pen Llŷn, North Wales and counts of *Buccinum undatum*.

Site	Area	Latitude	Longitude	Count	Site	Area	Latitude	Longitude	Count	Site	Area	Latitude	Longitude	Count
30	East Control	53.03363333	-4.489866667	51	**40**	North Control	53.06228333	-4.53685	6	**83**	Reef	53.00166667	-4.5327	178
31	East Control	53.059	-4.48145	19	**44**	North Control	53.06696667	-4.521316667	46	**84**	Reef	53.00525	-4.532116667	190
32	East Control	53.05718333	-4.50965	8	**46**	North Control	53.06936667	-4.524766667	15	**90**	Reef	53.0016	-4.53675	320
33	East Control	53.05338333	-4.506683333	44	**47**	North Control	53.06508333	-4.53015	52	**91**	Reef	53.00206667	-4.53445	143
43	East Control	53.06345	-4.495066667	83	**48**	North Control	53.06178333	-4.533916667	16	**92**	Reef	53.01728333	-4.5341	46
51	East Control	53.03111667	-4.484983333	58	**58**	North Control	53.05966667	-4.517366667	46	**93**	Reef	53.01931667	-4.530883333	120
53	East Control	53.0388	-4.50465	78	**59**	North Control	53.0639	-4.5226	15	**68**	South Control	52.96478333	-4.554266667	97
54	East Control	53.05681667	-4.470733333	32	**61**	North Control	53.06771667	-4.508783333	17	**69**	South Control	52.97686667	-4.55275	3
53a	East Control	53.02895	-4.497133333	39	**86**	North Control	53.05061667	-4.53965	14	**80**	South Control	52.96021667	-4.557866667	149
54a	East Control	53.03126667	-4.4865	22	**42**	Reef	53.01765	-4.54495	53	**81**	South Control	52.95816667	-4.555716667	35
55	East Control	53.02903333	-4.48005	144	**48a**	Reef	53.00235	-4.538783333	98	**86a**	South Control	52.96658333	-4.579516667	1
56	East Control	53.03318333	-4.494216667	20	**49**	Reef	53.01796667	-4.542683333	87	**87**	South Control	52.96861667	-4.582983333	18
57	East Control	53.03711667	-4.50515	10	**50**	Reef	53.02433333	-4.556233333	87	**88**	South Control	52.97278333	-4.56495	46
60	East Control	53.0541	-4.505166667	8	**62**	Reef	53.02415	-4.551133333	60	**89**	South Control	52.96821667	-4.565416667	0
34	North Control	53.0586	-4.520483333	24	**63**	Reef	52.99888333	-4.53305	64	**95**	South Control	52.97016667	-4.570333333	59
35	North Control	53.0639	-4.52715	51	**64**	Reef	53.00681667	-4.559616667	65	**96**	South Control	52.97298333	-4.5779	30
36	North Control	53.06891667	-4.513666667	57	**66**	Reef	53.01316667	-4.539083333	99	**97**	South Control	52.97346667	-4.5689	183
37	North Control	53.07258333	-4.519216667	3	**67**	Reef	52.99963333	-4.534766667	175	**98**	South Control	52.97591667	-4.573683333	1
38	North Control	53.06898333	-4.524016667	57	**70**	Reef	53.01146667	-4.544833333	103	**99**	South Control	52.97278333	-4.56495	45
39	North Control	53.06821667	-4.537116667	18	**82**	Reef	53.00063333	-4.537916667	149					

Appendix B2. Average *B. undatum* counts in each area

Area	Median count	Standard Deviation
East Control	31	36.49
North Control	17	20.12
Reef	99	68.82
South Control	40	61.17

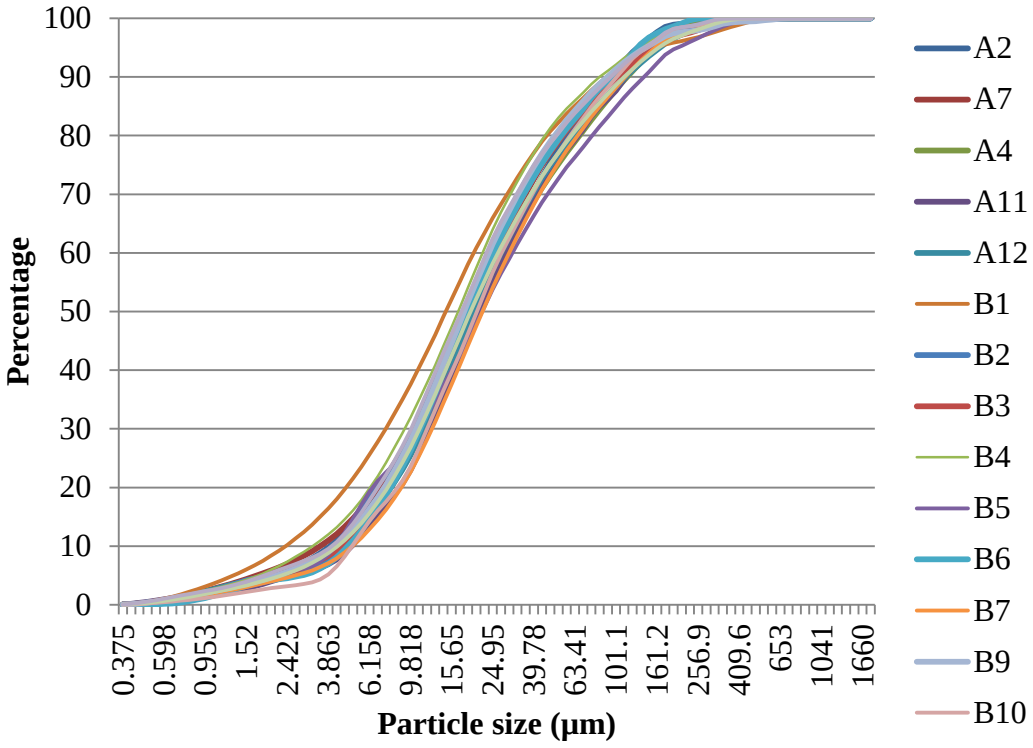
Appendix B3. Tukey post hoc comparisons including upper and lower confidence intervals for *B. undatum* counts in 4 areas off the Pen Llŷn, North Wales.

Areas	Lower	Upper	P value
North & East	-4.40	1.49	0.56
Reef & East	1.52	7.24	<0.001
South & East	-2.83	3.16	0.999
Reef & North	2.98	8.69	<0.001
South and North	-1.38	4.62	0.487
South and Reef	-7.13	-1.32	0.002

Chapter 4

Appendix C1. Total Particulate Matter and Organic material collected in experimental chambers. One scouring pad in a control box was lost during the experiment and one zip-lock bag containing a control scouring pad leaked; these two samples were not included due to low content.

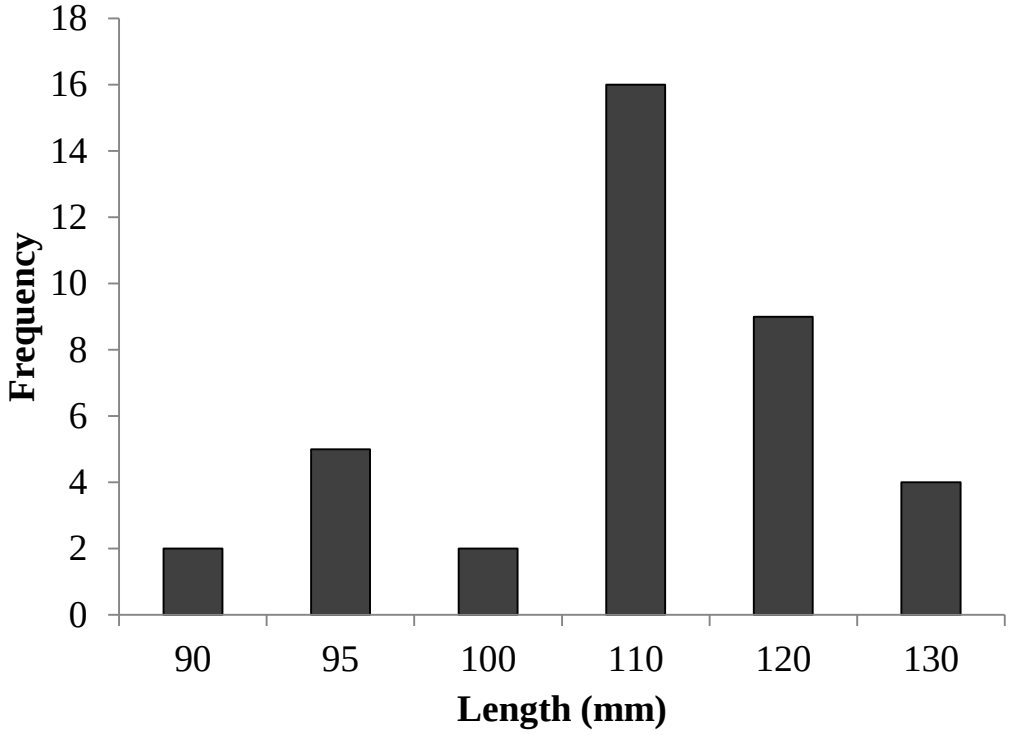
Treatment	Deposition TPM (gm^2)	Organic material (gm^2)
Control scouring pad	28.7	4.87
Control scouring pad	20.99	3.42
Control scouring pad	18.62	3.97
Control scouring pad	26.19	4.00
Control scouring pad	25.22	3.88
Control scouring pad	33.02	3.56
Control scouring pad	57.1	3.50
Control Box	56.49	9.81
Control Box	33.43	5.13
Control Box	36.88	6.18
Control Box	29.78	4.74
Control Box	21.82	3.70
Control Box	28.56	3.82
Control Box	30.49	4.56
Dead	39.72	6.32
Dead	48.41	7.16
Dead	58.08	10.09
Dead	45.68	6.54
Dead	27.23	5.74
Dead	39.31	6.44
Dead	57.25	10.84
Dead	47.6	7.84
Live	81.14	21.53
Live	53.07	9.68
Live	68.37	9.71
Live	58.88	16.26
Live	55.5	9.03
Live	61.13	9.06
Live	88.24	14.84
Live	48.99	7.86



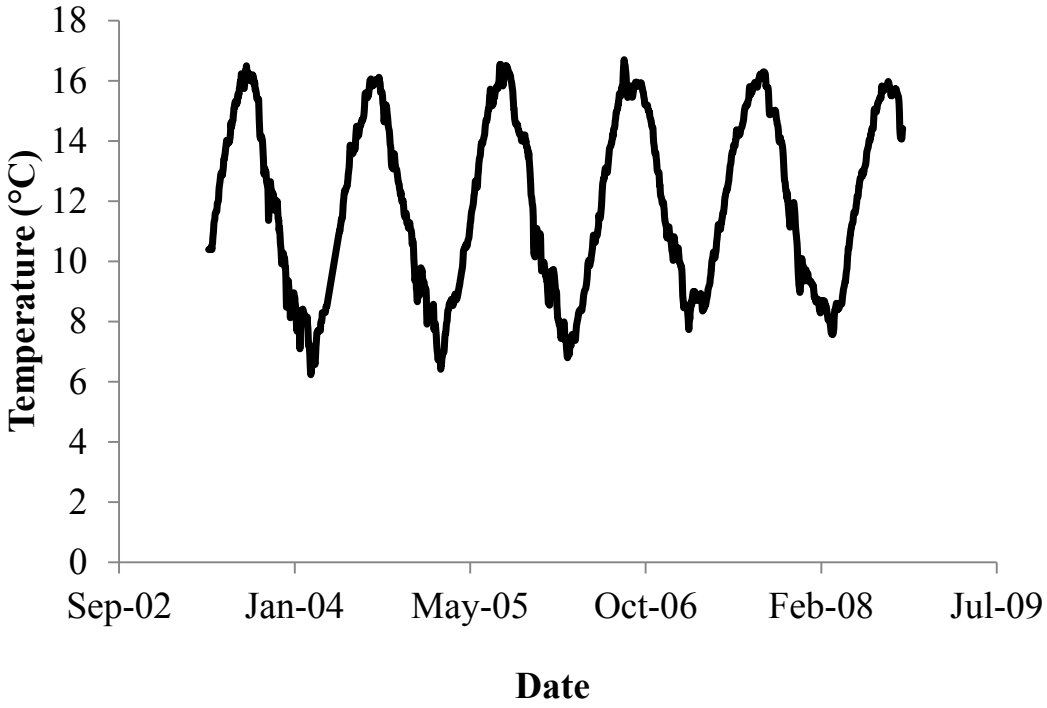
Appendix C2. Particle size distribution from *in situ* sediment samples collected from Port Appin *M. modiolus* reef (B1-12) and an off-reef control site (A2-12).

Appendix C3. Counts of animals that settled in the experimental chambers designed for collecting sediment left *in situ* on a *M. modiolus* reef for 7 days.

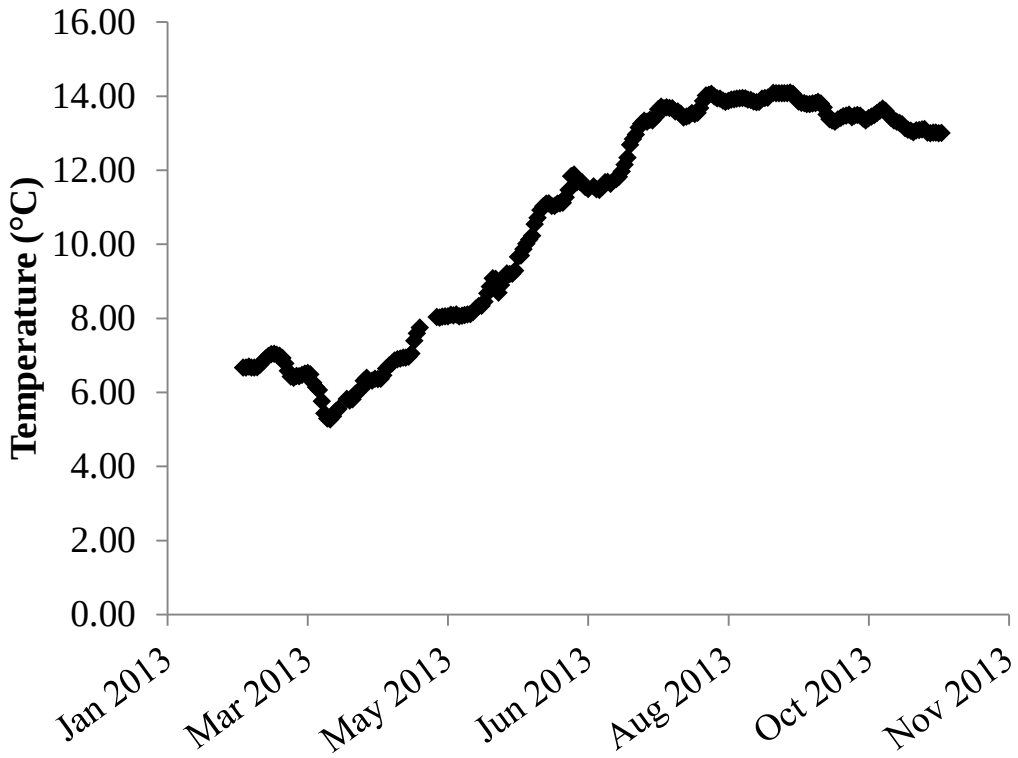
Sample	**Site**	**Treatment**	***Galathea intemidea***	***Palaemon serratus***	***Pisidia longicornis***
A4	Control	Control Box	0	0	0
A10	Control	Control Box	0	0	0
A11	Control	Control Box	0	0	0
A12	Control	Control Box	0	0	0
B4	Reef	Control Box	0	0	0
B8	Reef	Control Box	0	0	0
B9	Reef	Control Box	0	0	0
B11	Reef	Control Box	0	0	0
A2	Control	Dead	0	0	0
A3	Control	Dead	0	1	0
A7	Control	Dead	1	0	0
A9	Control	Dead	0	0	0
B5	Reef	Dead	1	0	0
B6	Reef	Dead	1	1	0
B10	Reef	Dead	1	0	0
B12	Reef	Dead	0	1	0
A1	Control	Live	0	1	0
A5	Control	Live	0	0	0
A6	Control	Live	0	1	0
A8	Control	Live	0	0	0
B1	Reef	Live	0	0	0
B2	Reef	Live	0	0	0
B3	Reef	Live	1	0	0
B7	Reef	Live	1	1	1



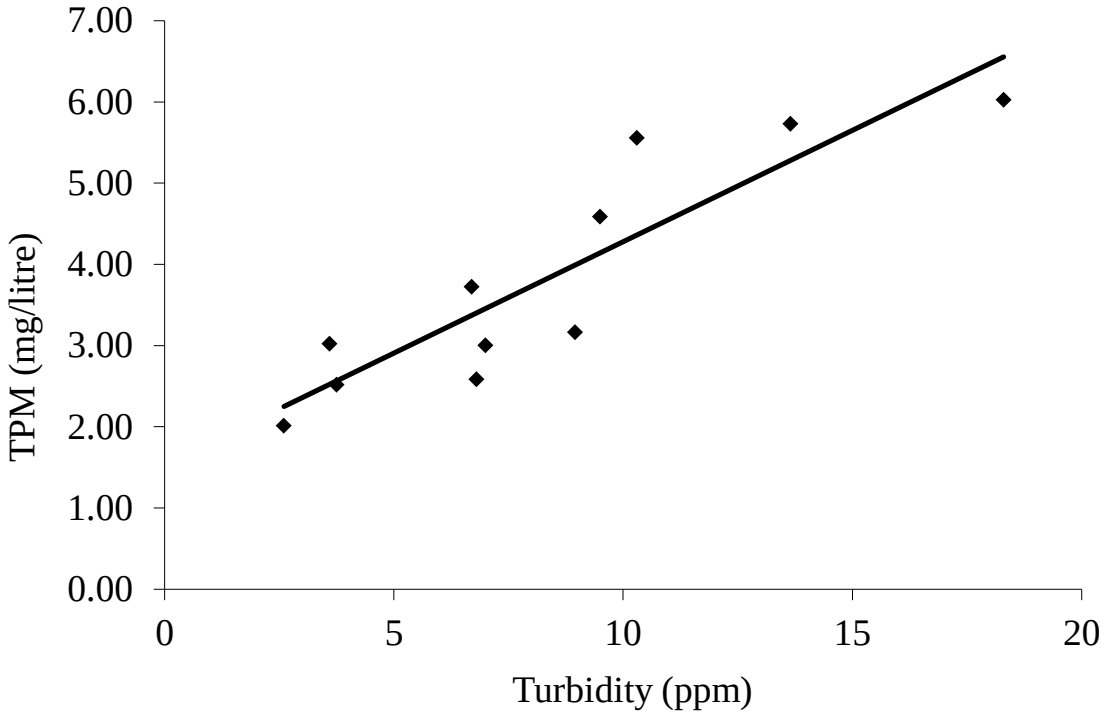
Appendix D1. Size frequency distribution of *M. modiolus* used in Experiment 1.



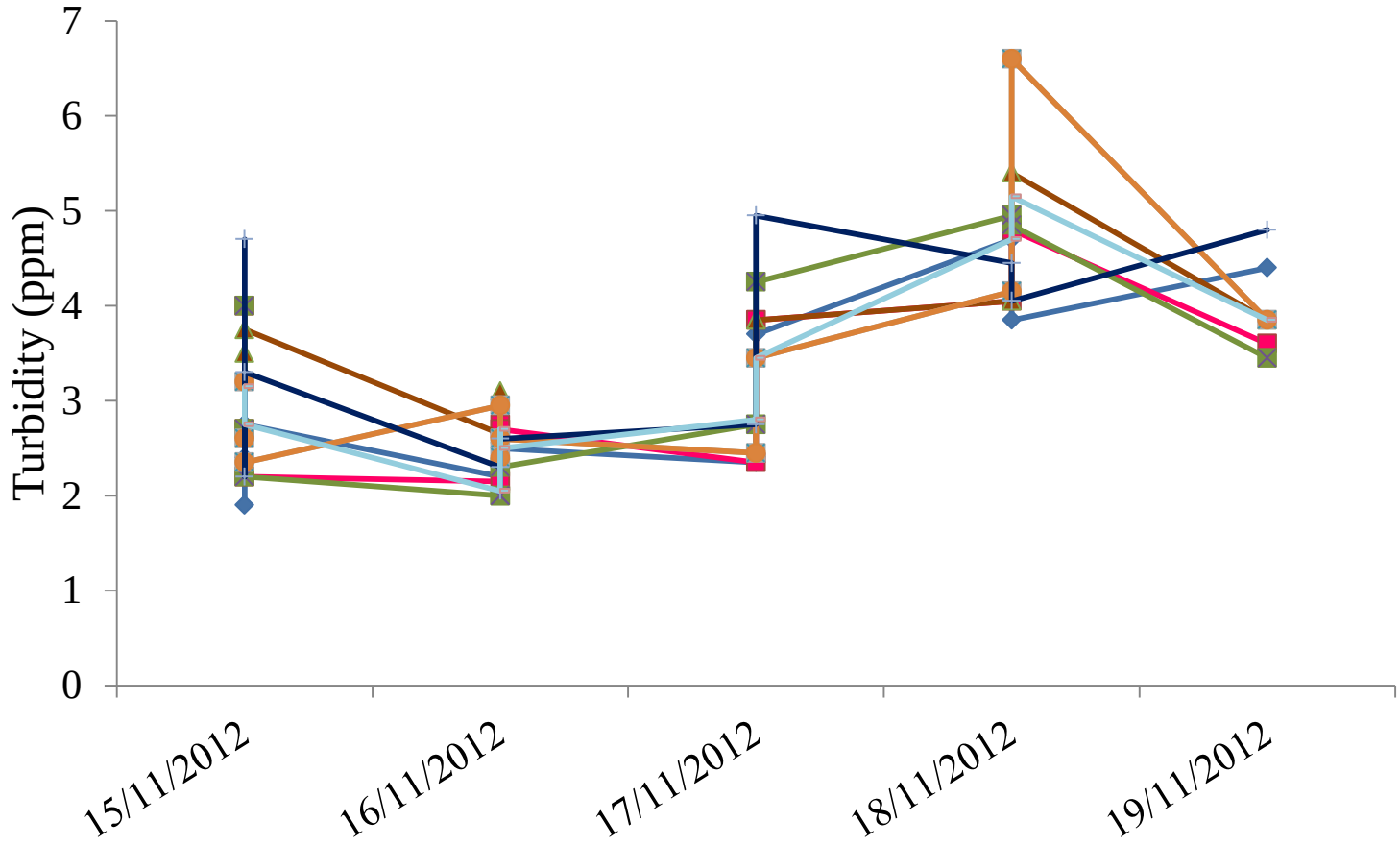
Appendix D2. Seabed temperature data from the Pen Llŷn *M. modiolus* reef in the Irish Sea.



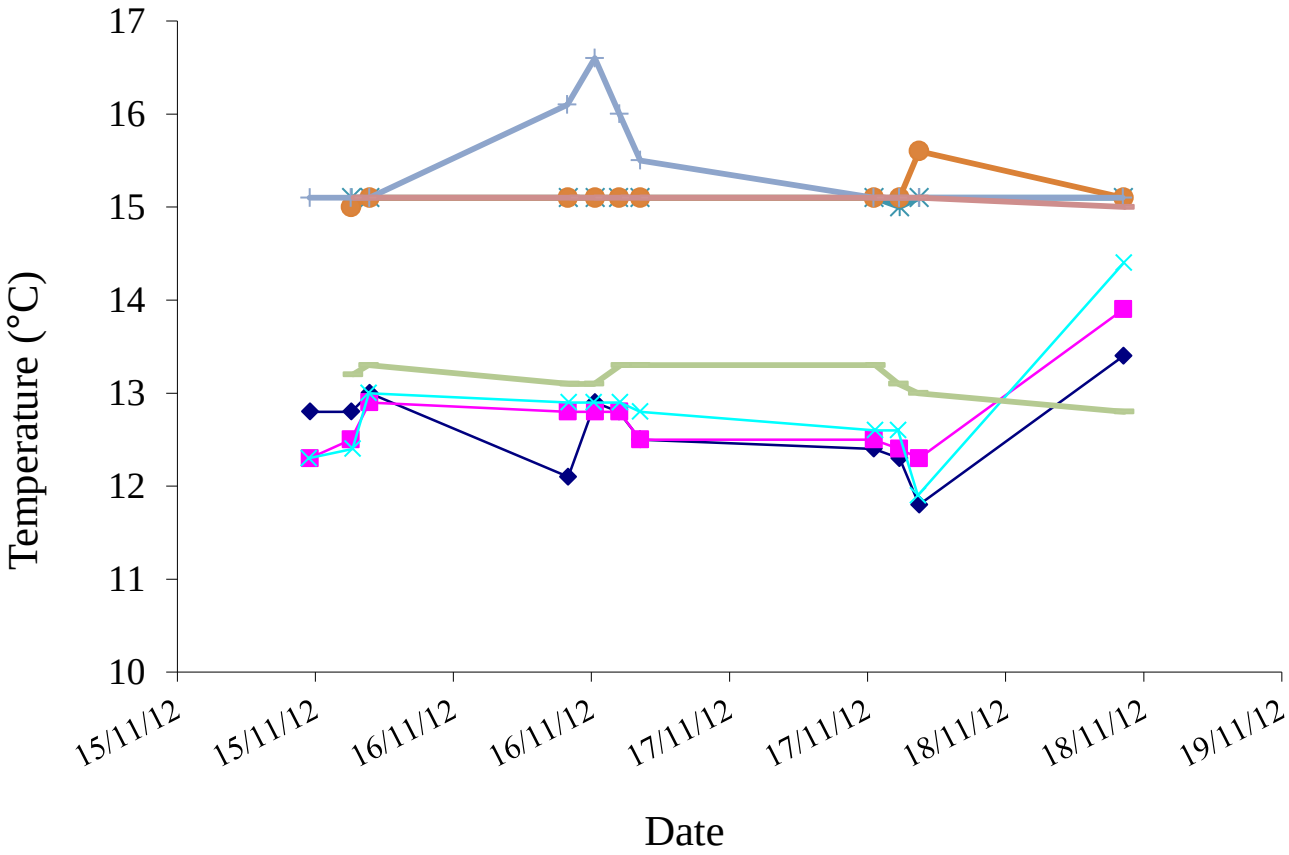
Appendix D3. Seabed temperature data from a *M. modiolus* reef in Loch Creran, Scotland.



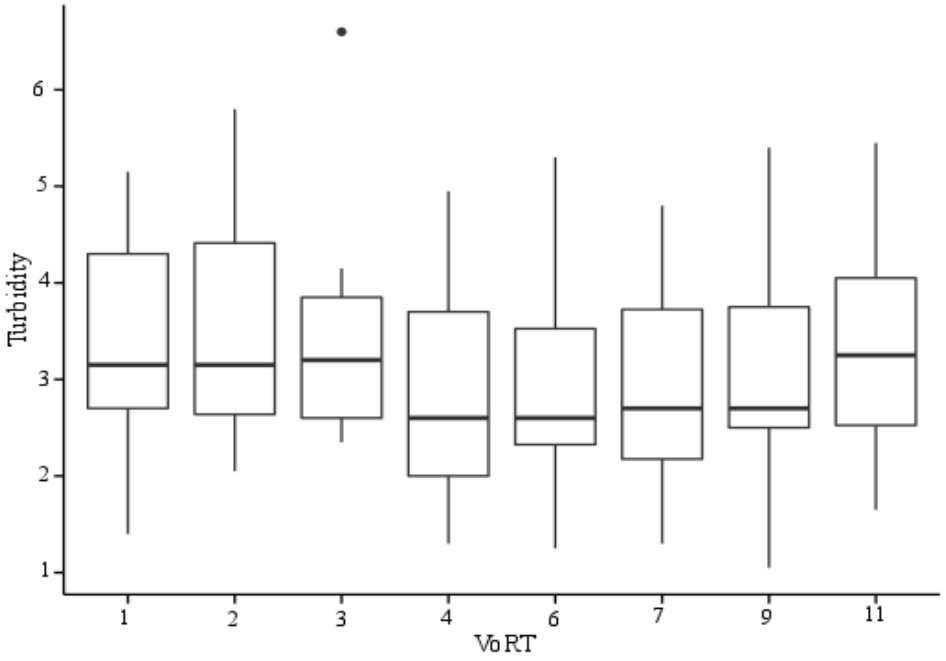
Appendix D4. Turbidity Calibration with Total Particulate Matter from three VoRTs, $R^2 = 0.799$.



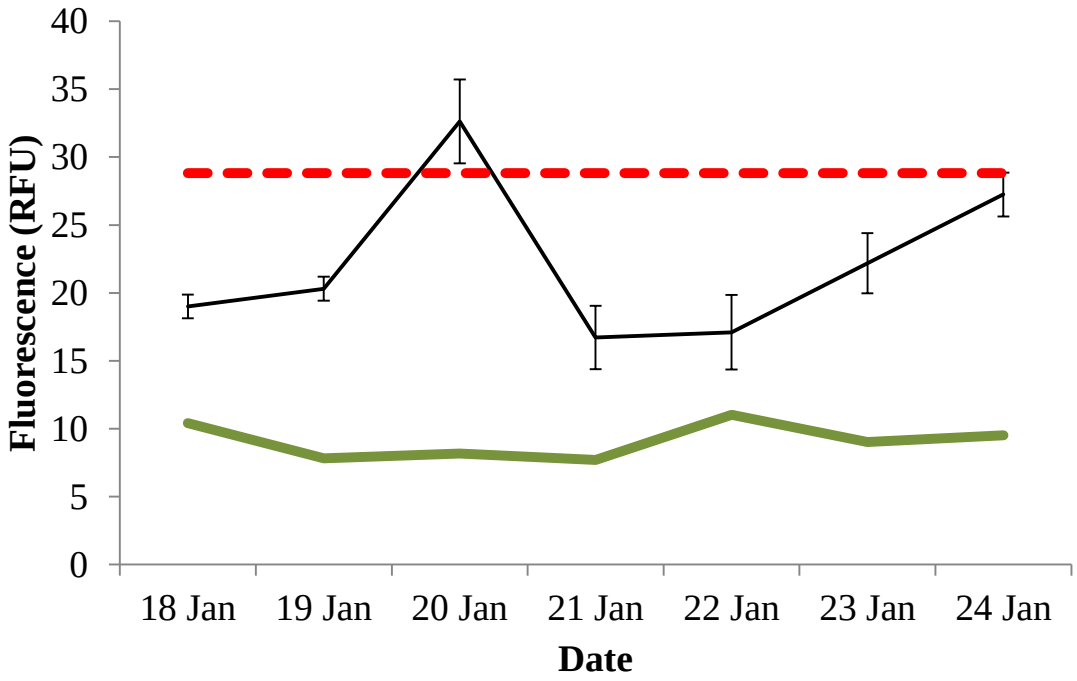
Appendix D5. Turbidity measurements from VoRTs during Experiment 1. Dark blue=VoRT 2; pink=VoRT 4; light blue=VoRT 11; turquoise=VoRT 1; orange=VoRT 3; grey=VoRT 6; brown=VoRT 7; green=VoRT 9.



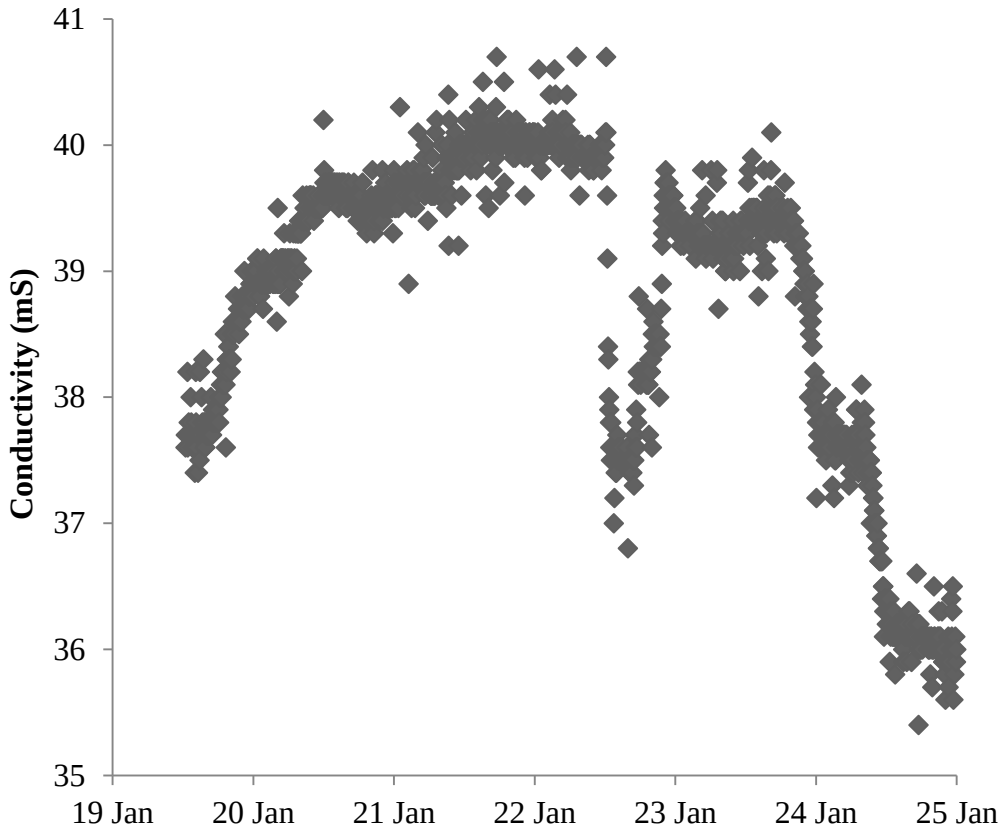
Appendix D6. Temperature in 8 VoRTs during Experiment 1. Dark blue=VoRT 2; pink=VoRT 4; bright blue=VoRT 11; turquoise=VoRT 1; orange=VoRT 3; grey=VoRT 6; brown=VoRT 7; green=VoRT 9.



Appendix D7. Turbidity (ppm) in each VoRT during Experiment 1 (n=11). The upper and lower edges of the boxes show the first and third quartiles and outliers are plotted as solid points.



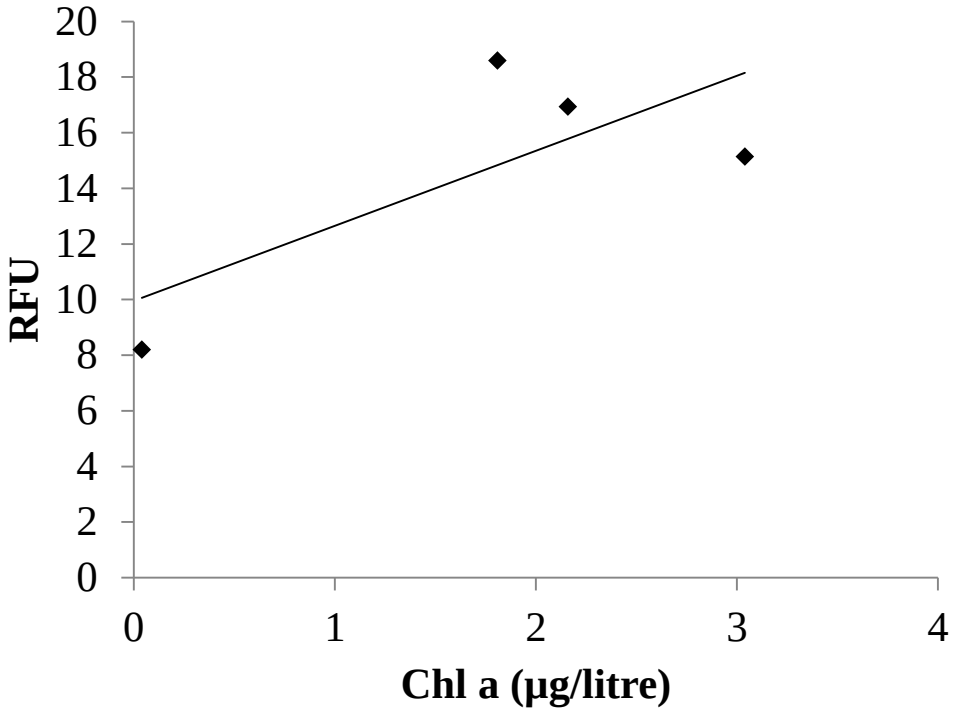
Appendix D8. Average fluorescence readings from 12 VoRTs measured throughout trial 3 (black line), error bars show 1SE. Green line shows seawater fluorescence measured from the header tank supplying the VoRTS. Red dashed line shows the target fluorescence to achieve chlorophyll a concentrations of 7µg l^{-1}.



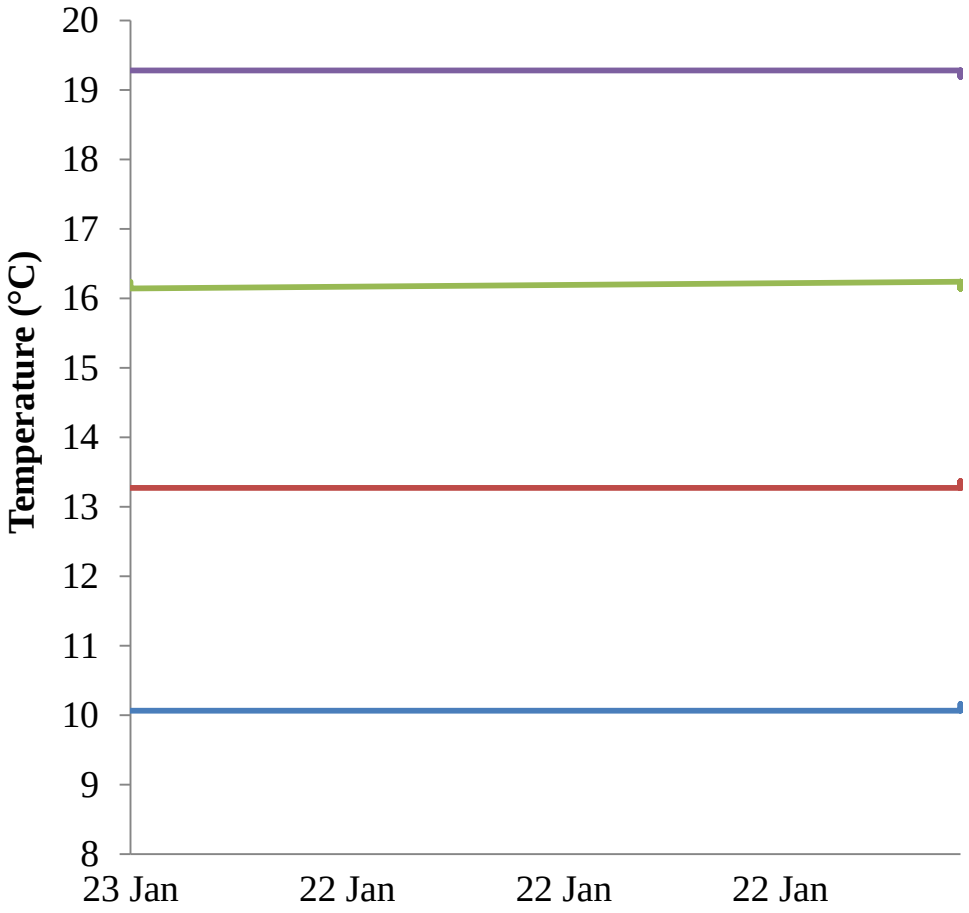
Appendix D9. Seawater conductivity in the header tank supplying the VoRTs with seawater throughout Experiment 2 (January 2015). Units are in milli-siemens per cm (mS) where conductivity of 38mS corresponds to an absolute salinity of 35.2 g/kg.

Appendix D10. Protocol used for chlorophyll extractions

- Acetone is diluted with MilliQ water to make a 90% solution
- Filter a known volume of sample onto A/E Glass fibre filters 25mm dia.
- Keep a record of volume filtered as this is required at the Fluorometer
- Place the filter paper into a 15ml screw cap centrifuge tube
- Add 8mls 90% acetone.
- Cover with foil and leave in the fridge overnight for the extraction to take place
- Obtain a box of ice
- Keep samples cool and dark (ice and foil)
- Use MSE Soniprep 150 to sonicate for 1 min on high (amplitude 3)
- Clean probe with acetone between each sample
- Use Eppendorf Centrifuge 5810R to centrifuge for 6 mins at 4000RPM
- Use Turner Designs Trilogy Fluorimeter
- Ensure the Chl A Acid module is in place
- Pour some supernatant into the glass cuvette and insert in the Fluorometer
- Calibration done saved in machine as 'Measure Calibration Chris 26'
- Follow on screen instructions (needs filtered volume and extracted volume (8ml)
- Click “read Fb”
- Add 50uL HCl to acidify the solution
- Click “read Fa”
- Gives Chl A and Pheophytin in µg/l



Appendix D11.Calibration of Chlorophyl a and Relative Fluorescence Units (RFU) used to achieve natural algae concentrations in Experiment 2.



Appendix D12. Temperature readings from 4 temperature loggers placed in 1 of 3 temperature replicate VoRTs during Experiment 2. Purple = 19°C, green=16°C, red = 13°C, blue = 10°C.

Appendix D13. Summarised parameters of the mixed effects models used in Experiment 3.

Response	Fixed Factors	Random Factors	Deviance	AIC
Biodeposition	Null	VoRT	62.26	68.26
	Temperature		51.83 *	63.84
	Sex		51.57	65.57
	Temperature*Sex		43.01 *	63.01
Byssus	Null	VoRT	102.61	108.61
	Temperature		92.83 *	104.83
	Sex		88.12 .	102.12
	Temperature*Sex		85.91	105.91

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ‘ ’ 1

Chapter 6

Appendix E1. Sediment sequestration scaled up for the Appin reef and the proportion of carbon within this (10%).

Sediment deposition enhancement		**Proportion of Carbon only**	
gm^2 per week	32	g C per m^2 per day	3.25
gm^2 day	5	g C per m^2 per week	0.464
gm^2 year	1694	g C m^2 year	169
g per year at Appin	33 880 834	g C m^2 year at Appin	338 8083
kg per year at Appin	33 881	kg per year at Appin	3388